Malacothamnus

Volume 1

Keir Morse

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A Morphological Assessment of Taxonomic Boundaries in the Genus *Malacothamnus* (Malvaceae)

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A Morphological Assessment of Taxonomic Boundaries in the Genus *Malacothamnus* (Malvaceae)

Author: Keir Morse
www.keiriosity.com

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Author's Note

The three volumes of this *Malacothamnus* monograph mostly follow the three chapters of my PhD dissertation but with multiple revisions and additional peer review. The earlier dissertation version of this work should be viewed as an unfinished draft of what is presented here.

Three major goals in self-publishing my *Malacothamnus* research were to provide all the details future *Malacothamnus* researchers may need for their research, provide a large amount of color figures, and to make it all freely available to anyone who wanted it without spending thousands of dollars to do so. These goals are at odds with the way most academic publishing works at present and I could not find a journal that met the requirements necessary for these publications.

Regarding peer-review, I was faced with trying to satisfy multiple audiences that wanted different things out of these publications. Some people wanted all the details of the analyses and the evidence I used in making taxonomic decisions related to *Malacothamnus*. Some wanted a highly abridged form of this. Some just wanted the taxonomic treatment with lots of photos and some basic information about the genus. I can satisfy the first and last of those groups and I attempt to do so in this three-volume, open-access monograph of the genus. Those who want a highly abridged account can start with the abstracts and Volume 3, and then dig deeper into Volumes 1 and 2 if further interested.

Volume 1 is a morphological assessment of *Malacothamnus* to clarify how morphologically distinct previously described taxa and possible undescribed taxa are. These analyses resulted in specimen groupings with varying degrees of morphological and geographic cohesion, most of which align with previously described taxa.
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Volume 2 uses phylogenetic analyses to test the morphological groupings from Volume 1 as hypothesized lineages. The resulting evidence from both morphological and phylogenetic analyses are then used to make taxonomic decisions for the treatment in Volume 3. Areas where further research is needed are noted and three new species are described.
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Volume 3 is a new treatment of *Malacothamnus*, which includes preliminary conservation assessments of each taxon and natural history information related to the genus. It also summarizes some of the findings in Volumes 1 and 2 for those who do not wish to delve into the details in those volumes.
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ABSTRACT

The taxonomy of the genus *Malacothamnus* (Malvaceae) has been controversial for many years due to conflicting treatments and the many taxa of conservation concern not recognized in some of these treatments. Purported intergradation and hybridization are the primary justifications for not recognizing these taxa. Two recent morphological studies examining small subsets of *Malacothamnus* taxa debunked the purported ambiguities between the taxa analyzed and provided evidence for a new species. This indicated a morphological assessment of the full genus would be highly beneficial to identify and clarify both morphological groupings and character states within the genus prior to testing taxon hypotheses within a phylogenetic framework.

This study follows the previous two by examining the remaining subsets of *Malacothamnus* taxa that have been combined and/or confused in the past. These subsets are analyzed with principle component analysis (PCA), pairwise permutational multivariate analysis of variance (PERMANOVA), and linear discriminant analysis (LDA) to answer (1) whether taxa relegated to synonymy by some authors are morphologically distinct or not, (2) whether there is morphological evidence to support purported intergradation between taxa, (3) whether previously defined morphological boundaries between taxa are justifiable or need refining, and (4) whether populations of hypothesized novel taxa are morphologically distinct from the taxa they have been included within.

Twenty-nine previously named and nine unnamed morphological groupings were recovered in taxon subset analyses. These were then included in a global analysis of the genus followed by comparisons of morphological characters between all groupings. The 38 morphological groups recovered range in distinctness from clear taxa that are both morphologically and geographically distinct to intergrading forms needing further research to base taxonomic decisions upon. These 38 morphological groups are assessed as hypothetical lineages using phylogenetic analyses in Volume 2 of this monograph.

Note: *M.* is used only to abbreviate *Malacothamnus*. All other genera starting in M are always spelled out.

1 INTRODUCTION

Malacothamnus Greene (Malvaceae), which is monophyletic within the *Malacothamnus* Alliance (*Malacothamnus*, *Iliamna*, and *Phymosia*), is a genus of generally short-lived, fire-following shrubs found primarily in the California Floristic Province (Bates 1963; Slotta 2004). The taxonomy of the genus has been controversial for many years due to conflicting treatments and the many taxa of conservation concern not recognized in some of these treatments (Kearney 1951; Skinner et al. 1995; Slotta 2012; Bates 2015; CNPS 2022). This controversy is primarily a question of whether any of the many taxa subsumed into the 11 broadly defined species of Bates (1993, 2015) should be recognized and, if so, which ones. All basionyms attributable to the genus as well as how the relatively recent authors Kearney (1951, 1955), Bates (1963, 1993, 2015), and Slotta (2004, 2012) treated them are shown in Fig. 1. To resolve the question of which taxa should be recognized, both molecular and morphological analyses have been employed but with only limited success (Bates 1963; Benesh and Elisens 1999; Slotta 2004; Morse and Chester 2019; Morse 2021). Taxonomic and morphological work from Kearney (1951) onwards is highlighted below to illustrate what is currently known about the genus and why there is taxonomic controversy.

Kearney's (1951) *Malacothamnus* treatment was the first thorough treatment of all taxa currently placed in the genus and has been the standard treatment to follow for those who choose to recognize a higher number of taxa in the genus. This treatment was mostly followed by Munz and Keck (1959) in *A California Flora* and in Munz's (1974) *A Flora of Southern California*, which were the primary treatments for California plants prior to the 1993 edition of *The Jepson Manual* (Hickman 1993). These California treatments include all species in the genus except for two Baja California, Mexico endemics: *M. foliosus* and *M. paniculatus*. The Kearney and Munz treatments are still mostly followed with respect to *Malacothamnus* taxa of conservation concern in California as 10 taxa with conservation status were subsumed into broader taxa in *The Jepson Manual* without clear evidence of their lack of distinction (CNPS 2022). Kearney, however, also did not offer clear evidence in his treatment and notes "Delimitation of several of the species is difficult and numerous specimens are intermediate in their characters."

Due to conflicting taxonomic treatments within *Malacothamnus* and the difficulties in taxon delimitation noted by Kearney (1951), Bates (1963) performed the first explicit quantitative study of morphological characters in the genus. However, while he notes that he performed analyses, he doesn't show either data or numerical results, and only notes some of the measurements analyzed. He summarizes that the characters analyzed for the taxon delimitation are "extremely variable in expression within taxa" and that no single character or measurement can consistently segregate any one taxon from the rest. He also notes that some of these characters are useful in combination, especially the calyx and calyx bracts (Bates called these involucral bracts in 1963 and involucellar bractlets in later treatments). Bates (1963) found much intergradation of characters between the 28 taxa of Kearney (1951, 1955) but some morphological discontinuity between 11 groupings, each including one or more of Kearney's taxa. Based on this, purported hybridization in the wild, and crossing experiments showing little reproductive barriers in the genus beyond geographic isolation, his treatments recognized only 11 taxa in what is currently circumscribed as *Malacothamnus* (Fig. 1). Bates

Basionym with year published
Kearney (1951, 1955)
Slotta (2004, 2012)
Bates (1993, 2015)
Malvastrum abbottii Eastw. (1936)
M. abbottii (Eastw.) Kearney
M. abbottii
M. abbottii
Malvastrum aboriginum B.L.Rob. (1897)
M. aboriginum (B.L.Rob.) Greene
M. aboriginum
M. aboriginum
Malvastrum clementinum Munz & I.M.Johnst (1924)
M. clementinus (Munz & I.M.Johnst.) Kearney
M. clementinus
M. clementinus
Malvastrum davidsonii B.L.Rob. (1897)
M. davidsonii (B.L.Rob.) Greene
M. davidsonii
M. davidsonii
Malvastrum densiflorum S.Watson (1882)
M. densiflorus (S.Watson) Greene var. densiflorus
M. densiflorus
M. densiflorus
Malvastrum viscidum Abrams (1907)
M. densiflorus var. viscidus (Abrams) Kearney
Malva fasciculata Nutt. ex Torr. & A.Gray (1838)
M. fasciculatus (Nutt. ex Torr. & A.Gray) Greene var. fasciculatus
M. fasciculatus var. fasciculatus
M. fasciculatus
Malvastrum thurberi A.Gray (1854)
Malvastrum splendidum Kellogg (1855) and Malvastrum thurberi var. laxiflorum A.Gray (1886)
M. fasciculatus var. laxiflorus (A.Gray) Kearney
Malvastrum parishii Eastw. (1936)
M. parishii (Eastw.) Kearney
Malvastrum nesioticum B.L.Rob. (1897)
M. fasciculatus var. nesioticus (B.L.Rob.) Kearney
M. fasciculatus var. nesioticus
Malacothamnus nuttallii Abrams (1910)
M. fasciculatus var. nuttallii (Abrams) Kearney
M. fasciculatus var. nuttallii
Malvastrum catalinense Eastw. (1936)
M. fasciculatus var. catalinensis (Eastw.) Kearney
M. fasciculatus var. catalinensis
Malveopsis arcuata Greene (1894)
M. arcuatus (Greene) Greene
?
Malvastrum hallii Eastw. (1936)
M. hallii (Eastw.) Kearney
M. hallii
Sphaeralcea fasciculata var. elmeri Jeps. (1936)
Malvastrum mendocinense Eastw. (1939)
M. mendocinensis (Eastw.) Kearney
Malvastrum foliosum S.Watson (1885)
M. foliosus (S.Watson) Kearney
?
M. foliosus
Malvastrum marrubioides var. paniculatum A.Gray (1886)
M. paniculatus (A.Gray) Kearney
M. paniculatus
Malvastrum fremontii Torr. ex. A.Gray (1849)
M. fremontii (Torr. ex A.Gray) Greene
M. fremontii
M. fremontii
Malvastrum howellii Eastw. (1936)
M. howellii (Eastw.) Kearney
Malvastrum howellii var. cordatum Eastw. (1936)
Malvastrum fremontii var. cercophorum B.L.Rob. (1897)
Malvastrum helleri Eastw. (1936)
M. helleri (Eastw.) Kearney
Sphaeralcea fremontii var. exfibulosa Jeps. (1936)
Malvastrum orbiculatum Greene (1891)
M. orbiculatus (Greene) Greene
M. orbiculatus
Malvastrum jonesii Munz (1925)
M. jonesii (Munz) Kearney
M. jonesii
M. jonesii
Malvastrum dudleyi Eastw. (1936)
Malvastrum gracile Eastw. (1936)
M. gracilis (Eastw.) Kearney
Malvastrum niveum Eastw. (1936)
M. niveus (Eastw.) Kearney
Malvastrum marrubioides Durand & Hilg. (1855)
M. marrubioides (Durand & Hilg.) Greene
M. marrubioides
M. marrubioides
Malvastrum gabrielense Munz & I.M.Johnst. (1925)
Malvastrum palmeri S.Watson (1877)
M. palmeri (S.Watson) Greene var. palmeri
M. palmeri var. palmeri
M. palmeri
Malacothamnus palmeri var. lucianus Kearney (1955)
M. palmeri var. lucianus
Malvastrum involucratum B.L.Rob. (1897)
M. palmeri var. involucratus (B.L.Rob.) Kearney
M. palmeri var. involucratus
Malacothamnus enigmaticus K.Morse & T.Chester (2019)
(published after all treatments)

Figure 1. Taxonomic flowchart showing all basionyms currently included within the genus *Malacothamnus* and how each was treated by Kearney, Slotta, and Bates. *Malacothamnus* is abbreviated as *M.* for these treatments. *Malvastrum splendidum* and *Malacothamnus fasciculatus* var. *laxiflorus* are homotypic. Bates's species on the right represent the broadest published circumscriptions of *Malacothamnus* taxa by any author and the groupings where confusion lies between included taxa. Question marks denote two taxa where it is unclear how Slotta intended to treat them (discussed later). Bates's unpublished 1963 treatment recognized all species from his 1993 and 2015 treatments as subspecies of *M. fasciculatus*.

never published the study or treatment presented in his 1963 dissertation but published a similar treatment 30 years later in *The Jepson Manual* (Bates 1993) and a slightly revised version of that for the *Flora of North America* (Bates 2015). The three Bates treatments offer the broadest species circumscriptions of any author with each species separated from the others by combinations of morphological characters. A major contribution of Bates's study of the morphological variation in *Malacothamnus* was common garden experiments where he concluded that much of the variation is genetic rather than environmental. Plants grown from seed in a common garden retained the morphological distinctions of their place of origin.

Two years after the publication of Bates' 1993 treatment, which subsumed many taxa listed as rare in California into more broadly defined and wide-ranging species, a journal article was published highlighting the research needs for conserving California's rare plants (Skinner et al. 1995). This article showed *Malacothamnus* to be the genus with the highest level of taxonomic uncertainty among plants listed as rare by the California Native Plant Society with 12 out of 16 *Malacothamnus* taxa (75%) on the rare plant list ranked as taxonomically uncertain (Skinner and Pavlik 1994). In response, Benesh and Elisens (1999) performed cluster, ordination, and statistical analyses of 26 morphological characters of nine taxa in the genus to identify characters that discriminate between taxa and to test hypotheses of taxon delimitation of species and varieties. This study focused on the five varieties of *M. fasciculatus* recognized by Kearney and four additional species from southern California as recognized by Bates, three of which were presumed by Bates to intergrade with *M. fasciculatus* (*M. davidsonii*, *M. densiflorus*, and *M. fremontii*) and the fourth being the disjunct San Clemente Island endemic *M. clementinus*. While this study did indicate utility in some characters measured, the authors note that polymorphism among species was extensive and that they did not identify any well-defined morphological and geographic clusters among the specimens sampled. They also note that many vegetative characters are too variable and difficult to quantify for analyses. As a result, they recommended employing molecular markers to investigate further. Possibly problematic in this study is the small sample size (46 specimens for nine possible taxa), which may not have been large enough to detect patterns in highly variable taxa with overlapping morphological characters. Identification of specimens may also have been problematic. I reviewed some of the specimens included in this study and found that misidentified specimens, possible undescribed taxa, and possible hybrids were included. This likely further confused interpretation of their results.

Slotta (2004) examined both molecular and morphological variation in *Malacothamnus* and the related genus *Iliamna* Greene. While her molecular work did not resolve any questions of taxon delimitation within *Malacothamnus* or relationships between taxa in the genus, her morphological work greatly improved upon the study of Benesh and Elisens (1999) by expanding both the sampling of taxa and refining some of the characters measured. Slotta attempted to examine all taxa within the genus, measuring 419 specimens and 27 morphological characters. Slotta chose to quantitatively assess several of the qualitative characters used by Benesh and Elisens noting they could benefit from both quantitative and statistical analyses. Slotta analyzed her data using both unweighted pair-group method using arithmetic averages (UPGMA) and multidimensional scaling (MDS). Based on these analyses, she resurrected two species and four varieties in her *Malacothamnus* treatment in the 2nd

edition of *The Jepson Manual* that had been subsumed by Bates in the previous edition (Bates 1993; Slotta 2012). While Slotta seemingly clarified some taxonomic questions in the genus, her published key to the genus furthered confusion by including ambiguous couplets (ex: "Branches spreading or ± erect" vs. "Branches spreading"). Likewise, some of her herbarium specimen annotations made little sense related to the presumed geographic ranges of the taxa assigned.

A taxonomic question not directly addressed by Slotta was whether the disjunct populations of what Bates called *Malacothamnus aboriginum* in San Diego County, California should be considered the same species as the more northern populations near the type locality in San Benito County, California. Slotta removed San Diego County from the range of *M. aboriginum* in her treatments but did not clarify what taxon those plants actually should be assigned to (Slotta 2004, 2012). When examining specimens, Morse and Chester (2019) found the San Diego County plants to be clearly different from *M. aboriginum* and possibly either an undescribed species or a hybrid between the other San Diego County species *M. densiflorus* and *M. fasciculatus*. To assess this, they used the characters Slotta found most useful in taxon delimitation, while refining and adding others. Two major additions were the quantifying of Slotta's qualitative stem trichome density as well as defining and measuring stipular bracts. Using principal component analysis (PCA), they showed the questionable populations to be both morphologically and geographically distinct from the other three species examined and described these plants as the new species *M. enigmaticus*.

After assessing specimens of all *Malacothamnus* taxa to develop a set of characters targeting maximum differentiation between taxa, Morse (2021) tested these characters on the *M. palmeri* complex, which is distinguished from the rest of the genus by generally having capitate to subcapitate inflorescences rather than the more typical spike-like or panicle-like inflorescences. This species complex includes the three varieties of *M. palmeri* as defined by Kearney (1951, 1955). These varieties purportedly intergraded and were thus treated by Bates (2015) as a single species with no infraspecific taxa recognized. Slotta (2012) treated them with an intermediate interpretation as two varieties. Using PCA and linear discriminant analysis (LDA), Morse showed these three varieties to be both morphologically and geographically distinct with no intermediates and thus raised *M. palmeri* var. *involucratus* and *M. palmeri* var. *lucianus* to the species rank as *M. involucratus* and *M. lucianus*.

The results of Morse and Chester (2019) and Morse (2021) indicated that using similar analyses to assess the full genus would be highly beneficial to clarify morphological groupings and character states associated with these groupings prior to testing taxon hypotheses within a phylogenetic framework. Purported intergradation and hybridization have confused taxon boundaries in the past and is the primary justification for recognizing fewer taxa (Bates 1963). These recent studies, however, show that morphological analyses can remove perceived ambiguities between at least some previously confused taxa and may also provide evidence for novel taxa.

This study follows Morse and Chester (2019) and Morse (2021) in examining subsets of *Malacothamnus* taxa that have been combined and/or confused in the past to answer (1) whether taxa relegated to synonymy by some authors are morphologically distinct or not, (2) whether there is morphological evidence to support purported intergradation between taxa, (3)

whether previously defined morphological boundaries between taxa are justifiable or need refining, and (4) whether populations of hypothesized novel taxa are distinct from the taxa they have been included within. After clarifying morphological groupings within each of these subsets, all resulting morphological groupings are included in a global analysis of the full genus and morphological characters are compared between all groupings. The clarified morphological groupings and character states of each provide a morphological baseline for and hypotheses to test in the phylogenetic assessment of the full genus in Volume 2 of this monograph.

2 MATERIALS AND METHODS

2.1 Sampling

Malacothamnus generally germinate after fires and are often short-lived. Due to this, populations may seemingly disappear for decades until the next burn interval allows for germination. For example, only three populations incorporating a total of eight individuals were found of *Malacothamnus involucratus* during field surveys from 2017 to 2019 as most of its known range had not burned recently. As many populations are reduced to a soil seed bank at any particular time, a comparison of morphology for the full range of the genus relies heavily on herbarium specimens to supplement the geographic gaps where plants cannot currently be collected and to include morphological variation not observed during field surveys. As *Malacothamnus* are shrubs, some approaching six meters tall, this morphological assessment focuses only on the portion of the plant typically mounted on an herbarium voucher sheet. This includes the inflorescence and a portion of the stem with leaves below the inflorescence, sometimes including as little as a single node below the inflorescence.

I collected morphological data on 773 *Malacothamnus* specimens representing the full geographic and morphological range of the genus (Appendix 1). When enough were available, I measured 20 specimens within the circumscription of each basionym (Fig. 1) and each possible undescribed taxon under investigation. Additional specimens were measured in some especially variable taxa/groups. In some cases, multiple specimens were sampled from a single herbarium sheet or duplicates to account for high variation in measured characters within a population such as both spike-like and panicle-like inflorescences. Sampling of multiple specimens from a single population was also used to increase the sample size of those taxa with limited specimens. At least one type (holotype, lectotype, or isotype) was measured for all basionyms except for *Malveopsis arcuatus*, *Malvastrum fremontii* subsp. *cercophorum*, *Malvastrum splendens*, and *Malacothamnus enigmaticus*. Scanned images of these types were examined and specimens from near the type localities of *Malveopsis arcuatus, Malvastrum splendens,* and *Malacothamnus enigmaticus* were measured. The classification of each type measured (holo-, iso-, lecto-) is noted in Appendix 1.

2.2 Characters and Measurements

Measurements mostly follow Morse (2021), which uses a combination of characters found useful in previous studies and treatments as well as novel characters chosen based on reviewing specimens representing all named taxa in *Malacothamnus*. Forty-one characters were measured (Table 1). Fourteen of these characters were measured qualitatively and 27 quantitatively. Ten of the qualitative character measures are ordinal. Four are binary and assess the presence or absence of a character state. New characters to this paper that were not included in Morse (2021) include whether corollas dry open or closed following anthesis, presence/absence of ridge-like veins on the calyx lobes, and presence/absence of simple or bifurcate nonglandular trichomes on the abaxial side of the calyx. Below I include an explanation of the character of drying corollas. I also include further explanation of the stipular bract character and problems associated with this character when the full genus is considered.

A detailed discussion of all characters measured, including some methodological discussion, can be found in the "Utility of measured characters in distinguishing taxa" section of the Results/Discussion.

Table 1. Characters measured and explanations of measurements.

Character	Explanation
Inflorescence longest internode	Longest inflorescence internode (internodes numbered from 1 proximally and increasing distally; 0 if inflorescence capitate)
Inflorescence longest internode length	Longest internode in inflorescence (increment 1 mm)
Inflorescence longest branch length	Longest inflorescence branch, measured from main stem to farthest calyx tip (increment 1 mm)
Inflorescence type	Inflorescence type: capitate (0), subcapitate (1), spike (2), spike with proximal branches (3), borderline spike/narrow panicle (4), panicle (5)
Corollas drying	Corollas drying: closed (0), partially open (1), fully open (2), not assessable or unclear (X)
Calyx length	Calyx length from base of tube to tip of one lobe (increment 0.5 mm). A single calyx was measured per specimen and chosen based on intactness and quality of pressing.
Calyx lobe length	Calyx lobe length (increment 0.5 mm). A single lobe of the measured calyx was measured and chosen based on intactness and quality of pressing.
Calyx lobe width at widest	Calyx lobe width where widest (increment 0.5 mm)
Calyx lobe width at base	Calyx lobe width at base of calyx lobe (increment 0.5 mm)
Calyx lobe base to widest area	Distance from center of calyx lobe base to center of where calyx lobe is widest (increment 0.5 mm). Value = 0 if the calyx is widest at base.
Calyx lobe distance from tip where 1 mm wide	Distance from tip of calyx lobe to center of where calyx lobe expands to 1 mm wide (increment 0.5 mm)
Calyx bract length	Length of longest visible calyx bract below measured calyx (increment 0.5 mm)
Calyx bract width	Width of longest visible calyx bract below measured calyx (increment 0.1 mm)
Calyx bract color	Most common coloring based on all calyx bracts: green (0), partially red/black (1), all or mostly red/black (2).
Calyx trichomes ray length short	Length of shortest calyx stellate trichome ray (increment 0.1 mm); shortest ray from anywhere on abaxial side of calyx including margin
Calyx trichomes ray length long	Length of longest calyx stellate trichome ray (increment 0.1 mm); longest ray from anywhere on abaxial side of calyx including margin
Calyx trichomes ray length mean	Mean length of calyx stellate trichome rays (increment 0.1 mm); mean of a single measurement from 10 separate adjacent trichomes at the center of abaxial side of calyx lobe. Bias in choice of ray reduced by holding ruler at a single angle and only measuring those rays which most closely aligned with ruler.
Calyx trichomes glandular short	Length of shortest calyx glandular trichomes (increment 0.1 mm); shortest trichome from anywhere on abaxial side of calyx including margin; glandular trichomes <0.1 mm recorded as 0 mm
Calyx trichomes glandular long	Length of longest calyx glandular trichomes (increment 0.1 mm); longest trichome from anywhere on abaxial side of calyx including margin; glandular trichomes <0.1 mm recorded as 0 mm
Calyx trichomes glandular mean	Mean length of calyx glandular trichomes (increment 0.1 mm); mean of measurements from 10 adjacent trichomes at the center of abaxial side of calyx lobe; glandular trichomes <0.1 mm recorded as 0 mm
Calyx lobes with ridge-like veins	Calyx lobes with ridge-like veins on abaxial surface: no (0), slightly protruding (1), obviously protruding (2)

Character	Explanation
Simple or bifurcate trichomes	Simple or bifurcate nonglandular trichomes present abaxially on calyx: no (0), yes (1)
Calyx lobe surface visible	Calyx lobe surface visible through trichomes without magnification: no (0), slightly (1), clearly (2)
Calyx tube surface visible	Calyx tube surface visible through trichomes without magnification: no (0), slightly (1), clearly (2)
Stipular bract width	Width of widest stipular bract (increment 0.5 mm); if lobed, measure below lobes
Stipular bract length	Length of widest stipular bract (increment 0.5 mm); if lobed, length of longest lobe
Stem trichomes ray length short	Length of shortest stem stellate trichome ray (increment 0.1 mm); shortest ray from anywhere on 1st internode proximal to the inflorescence
Stem trichomes ray length long	Length of longest stem stellate trichome ray (increment 0.1 mm); longest ray from anywhere on 1st internode proximal to the inflorescence
Stem trichomes ray length mean	Mean length of stem stellate trichome rays (increment 0.1 mm); mean of a single measurement from 10 separate adjacent trichomes at the center of 1st internode proximal to the inflorescence. Bias between choice of ray reduced by holding ruler at a single angle and only measuring those rays which most closely aligned with ruler.
Stem trichomes glandular short	Length of shortest stem glandular trichomes (increment 0.1 mm); shortest trichome from anywhere on 1st internode proximal to the inflorescence; glandular trichomes <0.1 mm recorded as 0 mm
Stem trichomes glandular long	Length of longest stem glandular trichomes (increment 0.1 mm); longest trichome from anywhere on 1st internode proximal to the inflorescence; glandular trichomes <0.1 mm recorded as 0 mm
Stem trichomes glandular mean	Mean length of stem glandular trichomes (increment 0.1 mm); mean of measurements from 10 adjacent trichomes at the center of 1st internode proximal to the inflorescence; glandular trichomes <0.1 mm recorded as 0 mm
Stem trichomes rays visible without magnification	Stem stellate trichome rays discernable without magnification: no (0), slightly (1), clearly (2)
Green stem visible without magnification near inflorescence base	Stem visible through the trichomes without magnification near the inflorescence base: no (0), slightly (1), clearly (2)
Green stem visible without magnification distally in inflorescence	Stem visible through the trichomes without magnification near the distal end of the inflorescence: no (0), slightly (1), clearly (2)
Leaf trichomes adaxial mean	Mean of 10 distances between separate stellate trichome centers on adaxial leaf surface (increment 0.1 mm); Distance between trichomes was measured in a meandering line, measuring the closest stellate trichome to the previous without remeasuring any and moving as much as possible in a consistent direction away from the first trichome measured. When very sparse, all trichome distances may be measured, as well as distance of trichomes to the nearest edge of the leaf as a substitute for the nearest trichome when fewer than six trichomes are present.
Leaf trichomes abaxial mean	Mean of 10 distances between separate stellate trichome centers on abaxial leaf surface (increment 0.1 mm); see leaf trichomes adaxial mean for details
Leaf lobing	Degree of leaf lobing: none (0), slight (1), obvious (2)
Leaf base cordate	One or more leaves with subcordate to cordate base: no (0), yes (1)
Leaf base truncate	One or more leaves with truncate base: no (0), yes (1)
Leaf base cuneate	One or more leaves with subcuneate to cuneate base: no (0), yes (1)

The “corollas drying” character is not how a corolla dries when pressed, but how it naturally dries on the plant after anthesis. *Malacothamnus* corolla lobes are imbricate in bud. In most *Malacothamnus* taxa, they return to this state after anthesis and dry that way. Though similar, flowers that dried closed are easily distinguished from budding flowers on both live and herbarium specimens. After anthesis the corolla has a somewhat wrinkled and uneven appearance compared to its smooth and even appearance in bud. I have observed during field surveys that in a few taxa the corollas remain open when they dry. This is most easily observed on fresh specimens as the corollas are drying and can be somewhat difficult to assess on dry specimens without corollas that have clearly dried closed. This is occasionally complicated by some corollas drying ambiguously, which I’ve seen in purported hybrid zones between species with corollas drying in different ways and rarely in aberrant plants within populations that mostly dry closed. Specimens where this character was unclear or too immature to assess were scored as “not assessable or unclear”. In the analyses, those specimens scored as “not assessable or unclear” were assigned an imputed value of the most common state found in morphologically similar plants from the same geographic region.

There are no corolla measurements in this study beyond the assessment of how the corolla dries. While there certainly may be some utility in corolla measurements, Bates (1963) noted that the calyx and calyx bracts appeared to be the characters least modified by environmental factors and were possibly the most useful in delimiting taxa. I have occasionally observed wide variation of corolla sizes in *Malacothamnus* populations during field surveys and little variation in calyx size between those same flowers. I have also observed that the calyx and calyx bracts appear to be the least modified both by timing of the collection (flowering vs. fruiting) and by pressing the specimen. While most specimens have well-pressed and easy to measure calyces, specimens with well-pressed corollas are uncommon.

Before delving into stipular bracts, it is helpful to clarify that what I refer to as calyx bracts are a whorl of three linear to ovate bracts immediately below the calyx, which is collectively called the epicalyx. Stipular bracts, stipule-like bracts with no blade or petiole, are found along the stem between the calyx bracts and blade-bearing bracts or leaves. Stipular bracts were found very useful in analyses related to the *Malacothamnus palmeri* complex and *M. enigmaticus* (Morse and Chester 2019; Morse 2021). This character can easily separate those few taxa with particularly wide stipular bracts from the rest of the genus. As such, I measured the widest stipular bract visible on each specimen regardless of position in the inflorescence with a focus on identification utility rather than strict homology. While easy to measure in those taxa with larger stipular bracts, I’ve found that in some taxa with smaller stipular bracts that they can be early deciduous, which is problematic when measuring more mature inflorescences. Likewise, stipular bracts are apparently absent in a few specimens which have bracts resembling bladed leaves with stipules well into the inflorescence, the stipules of which are likely homologous with stipular bracts. In instances when I could not find a clear stipular bract on a specimen, I substituted this measurement with a stipule from a bladed bract in the inflorescence or the most distal leaf with a stipule. If all stipules had fallen off the specimen (only 3 specimens), stipular bract measurements were imputed for analysis based on morphologically similar plants from the same geographic region.

2.3 Analysis subsets

Specimens were first analyzed in a series of species subsets focused on clarifying morphological groupings within taxa that have been combined and/or confused in the past. Resulting finer-scale morphological groupings of all subsets were then analyzed collectively. The 11 species as recognized by Bates (Fig. 1) form the most broadly circumscribed morphological groupings within *Malacothamnus* published by any author to treat the full genus. Most specimens can easily be assigned to one of these broadly defined species or to the recently described *M. enigmaticus*. Thus, Bates's species plus *M. enigmaticus* represent a logical starting point for species subsets to be assessed for finer-scale morphological groupings (both previously defined and new hypotheses) before a global analysis of the genus.

This is further justified by my phylogenetic research on *Malacothamnus* (see Volume 2). With one exception, preliminary phylogenetic analyses of RADseq data showed that specimens assigned to the narrowly defined taxa of Kearney are either monophyletic or form exclusive clades only with other taxa included in the same broadly defined Bates species. While these exclusive clades contain taxa included in only a single of Bates's species, they don't necessarily include all taxa Bates included in the same species, which indicates some of the taxa Bates lumped into single species may be separate lineages that are morphologically convergent. These analyses support the following taxa as being distinct from all others: *M. abbottii*, *M. aboriginum*, *M. clementinus*, *M. davidsonii*, *M. fremontii* sensu Bates, *M. jonesii* sensu Bates, *M. marrubioides*, *M. palmeri* sensu Bates, and the taxa within *M. fasciculatus* sensu Bates excluding *M. fasciculatus* s.s. The exception is a clade including all specimens from San Diego County and Baja California, the subclades of which do not correspond to named morphological groups. This problematic clade includes *M. densiflorus* sensu Bates, *M. enigmaticus*, *M. fasciculatus* s.s., and *M. foliosus* sensu Bates. Many specimens collected from Baja California appear to be morphologically intermediate between species only occurring there and San Diego County, which may indicate geneflow that could confound phylogenetic analyses.

As specimens from San Diego County and Baja California form a single clade where included specimens do not correspond to a single species as recognized by Bates and as some specimens from this region are morphologically ambiguous between Bates's species, analyses were first done on all specimens from this region to clarify whether Bates's species plus *M. enigmaticus* are morphologically distinct there and whether the ambiguous Baja California specimens could be assigned to morphological groups. These analyses include all measured specimens of *M. densiflorus* sensu Bates, *M. enigmaticus*, *M. fasciculatus* s.s., and *M. foliosus* sensu Bates. Resulting morphological groupings were carried forward for further analyses.

Following the assessment of the San Diego County and Baja California specimens, which clarifies whether or not Bates's species are distinct there and which of these species the ambiguous Baja California specimens are most similar to, I analyzed subsets of Bates's species to answer finer-scale questions such as whether taxa relegated to synonymy by some authors are morphologically distinct or not, whether there is morphological evidence to support purported intergradation between included taxa, whether previously defined morphological boundaries between taxa are justifiable or need refining, and whether populations of hypothesized novel taxa are distinct from the taxa they have been included in. Subsets of taxa

analyzed include *M. fasciculatus* sensu Bates, two disjunct regions of *M. davidsonii*, *M. densiflorus* sensu Bates, *M. marrubioides* plus the morphologically similar *M. foliosus* sensu Bates, *M. fremontii* sensu Bates, and *M. jonesii* sensu Bates plus the morphologically similar *M. abbottii*. To form a more cohesive narrative, background and questions for each of the subsets are included in the results/discussion of the analyses associated with each.

The resulting morphological groupings from the subset analyses, as well as species in the recently clarified *M. palmeri* sensu Bates (Morse 2021) and the morphologically distinct and monophyletic species *M. aboriginum* and *M. clementinus*, are carried forward for analysis of the full genus and comparisons of morphological characters between groups. Figure 2 provides a simplified workflow showing sequentially which sensu Bates species plus *M. enigmaticus* are included in each set of analyses.

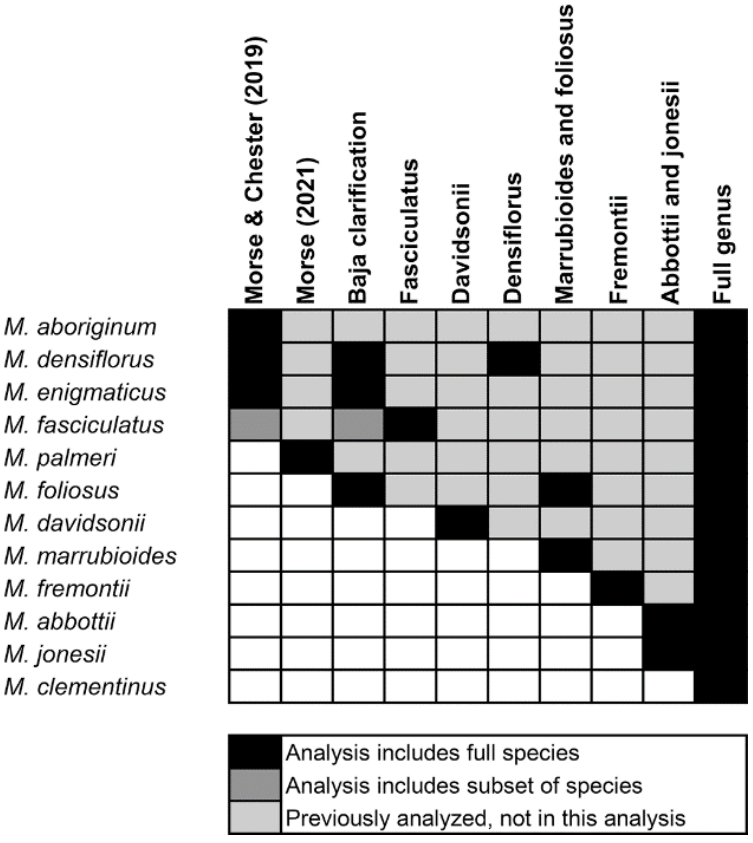

Figure 2. Analysis workflow showing *Malacothamnus* taxa included in the species subset analyses of this paper as well as Morse and Chester (2019) and Morse (2021). Rows are labelled with the species as recognized by Bates (2015) plus the recently described *M. enigmaticus* (Fig. 1). Columns show species subset analyses in sequential order and which species are included in each.

2.4 Analyses

Species subsets were analyzed with PCA, LDA, and pairwise permutational multivariate analysis of variance (PERMANOVA) to clarify finer-scale morphological groupings within each. All resulting morphological groupings from subset analyses were then included in PCA, LDA, and PERMANOVA of the full genus followed by a comparison of morphological distance and character measures between each morphological group. Sample sizes of the final morphological groupings in the subsets and the full genus analyses are included in the LDA results tables and Appendix 1.

In order to visualize clustering and intermediacy of specimens based on the morphological characters measured, PCA was performed using the *prcomp* function in R v. 4.0.2 (R Core Team 2020). Centered and scaled PCAs were plotted using base functions in R. When more than two hypothesized morphological groupings were compared without clear patterns for some groups, samples forming non- or mostly nonoverlapping clusters in PCAs were removed from the dataset and further PCAs were run with the remaining samples to assess for additional clustering. In cases where further clarification was needed and there were no nonoverlapping clusters, combinations of smaller numbers of morphological groups were used to see if clustering improved and to assess which morphological characters were most important in differentiating those groups. Outlier values of characters measured were not removed so as to assess the full variation within the dataset and to not bias against morphological groups with small sample sizes relative to others. While PCAs of data including both quantitative and qualitative characters are generally discouraged for statistical reasons, these PCAs were used only to explore clustering of morphological groups and to assess which characters contributed most strongly to these groupings. I tested an alternative PCA function in R designed specifically for mixed data types which yielded almost identical specimen clustering, but I rejected it as my ordinal categorical data could not be analyzed as ordinal and there was no combined and comparable output of quantitative and qualitative characters similar to traditional PCA character loadings. Character loadings for all PCA plots shown are in Appendix 2.

Initial classification of specimens for PCAs focused on assessing all previously named taxa and hypothesized undescribed morphological groupings. Specimen taxon assignment mostly follows the taxonomic divisions of Kearney (Fig. 1) who recognized the most taxa of any author to treat the full genus. Exceptions include undescribed groupings, vague Kearney groupings with a hypothesized clarification, basionyms not recognized by Kearney, and taxa clarified by Morse and Chester (2019) and Morse (2021). Basionyms not recognized by Kearney are assigned only to the type specimens of these taxa. Hypothesized undescribed groupings and clarified Kearney groupings are outlined in the species subset section they are analyzed within. Clarified Kearney groupings are based on extensive field surveys and review of specimens. To make patterns in PCAs more apparent when there are large numbers of taxa included, specimens in some PCAs are classified more broadly, usually following Bates (2015), to better illustrate a specific point. In all cases, classifications broader than Kearney's are noted.

To assess the utility of the morphological characters measured in classifying specimens to the morphological groupings recovered in PCAs, LDA was performed in R using the *lda* function in the *MASS* v. 7.3–51.6 package (Venables and Ripley 2002). LDA was run using leave-

one-out cross validation, rather than testing and training datasets, due to the relatively small sample sizes in each group.

To assess significance of the differences between each morphological group based on the characters measured, PERMANOVA was performed in R using the *pairwise.adonis* function in the *pairwiseAdonis* v. 0.0.1 package (Arbizu 2017) with 1000 permutations. Dissimilarities were generated using Gower's general coefficient of similarities (Gower 1971). P-values were adjusted using the False Discovery Rate (FDR) approach of Benjamini and Hochberg (1995). The Alpha level was set at 0.01. Adjusted p-values are rounded to three decimal places, the rounding of which does not change the significance of any. There is only a single degree of freedom for all pairwise comparisons, so this is excluded from the results tables.

A morphological distance matrix to compare relative distance between each morphological group in the genus was created using the *factoextra* v. 1.0.7 (Kassambara and Mundt 2020) and *usedist* v. 0.4.0 (Bittinger 2020) packages in R. Spearman correlation distance was generated for all specimen pairs using the *get_dist* function in *factoextra*. Distances between the centroids of morphological groups was then generated using the *dist_multi_centroids* function in *usedist*. This was then plotted with a heat map using *factoextra* to visualize morphological distance between groups more easily.

Boxplots showing the median, four quartiles of distribution, and outliers were prepared using base functions and the *ggplot2* (Wickham 2016) package in R to show discontinuity and relative degree of overlap in character measures between morphological groups. Scatterplots were prepared using base functions in R. Maps were generated in QGIS 3.10.7 (QGIS Development Team 2020). Adobe Acrobat and Adobe Photoshop were used to edit the layout and enhance clarity of some raw figures exported from R and QGIS.

3 ANALYSES

The Analyses chapter is divided into several sections, each focused on specific questions. The first section verifies the distinctness of Bates's species in San Diego County and Baja California and places morphologically ambiguous specimens from this area into morphological groupings for further analysis. This is followed by assessments of several subsets of species that have been combined and/or confused in the past as well as one subset examining two disjunct populations of a single species. The resulting finer-scale groupings from these analyses are then included in analyses of the full-genus. Character loadings for all PCA axes shown can be found in Appendix 2.

3.1 San Diego County and Baja California

While most *Malacothamnus* specimens are easily assigned to the broadly defined species of Bates (Fig. 1) or to the recently described *M. enigmaticus*, some ambiguous specimens from Baja California needed to be assessed before proceeding with species subset analyses as they did not clearly fit within one of those species. These unclear Baja California specimens were noted by Morse and Chester (2019), who sampled all the species from this region excluding *M. foliosus* sensu Bates and resolved *M. fasciculatus* s.s., *M. densiflorus* sensu Bates, and *M. enigmaticus* as morphologically distinct from one another. They, however, stated that their analyses indicated that much of what has been called *M. densiflorus* and *M. fasciculatus* in Baja California in the past may differ from those species and required further investigation. All specimens from this region were unresolved within a single clade in preliminary phylogenetic analyses, which further indicated a need for morphological assessment. This clade included *M. densiflorus* sensu Bates, *M. enigmaticus*, *M. fasciculatus* s.s., *M. foliosus* sensu Bates, and ambiguous specimens from the same region. Apparent morphological cohesiveness of the ambiguous specimens by geographic region indicated they could represent intermediates between adjacent species, undescribed species, or morphological extremes of described species. To assess this, I placed the unclear Baja California specimens into three hypothesized groups based on morphology and geography to clarify whether these groups actually are morphologically cohesive, which of the nearby species they are most similar to, and whether they are morphologically distinct from these species. These three groups are *M. fasciculatus*/*foliosus* intermediates, "Baja East", and "Baja East"/*fasciculatus* intermediates (Fig. 3).

The *M. fasciculatus*/*foliosus* intermediates are geographically intermediate between *M. foliosus* sensu Bates and the southernmost populations of *M. fasciculatus* sensu stricto. *Malacothamnus fasciculatus* s.s. has a spike-like inflorescence and relatively short, dense stellate trichomes. *Malacothamnus foliosus* sensu Bates has a spike-like to panicle-like inflorescence and relatively long, sparse stellate trichomes. The *M. fasciculatus*/*foliosus* intermediates appear most like *M. fasciculatus* s.s. overall but exhibit characters suggesting influence from *M. foliosus* such as panicle-like inflorescences as well as longer and sparser stellate trichomes. Not all *M. fasciculatus*/*foliosus* intermediates have all of these characters but always have one or more characters indicating possible intermediacy.

"Baja East" represents *Malacothamnus* specimens in Baja California that were similar to but did not cluster well with *M. enigmaticus* in the analyses of Morse and Chester (2019). Like *M. enigmaticus*, "Baja East" has relatively wide stipular bracts and very short and dense stellate trichomes on the stem. "Baja East" differs from *M. enigmaticus* in having many character measures generally smaller, though there is much overlap with *M. enigmaticus*. This indicates "Baja East" could be morphologically divergent populations of *M. enigmaticus*, an intermediate between *M. enigmaticus* and another species, or an undescribed lineage perhaps related to *M. enigmaticus*. Worth noting is a gap of 225 km between the northern and southern specimens of "Baja East". While no specimens in this gap resemble "Baja East", a few iNaturalist observations in the region do, indicating that the current specimens may represent the northern and southern extents of a largely unsampled distribution (iNaturalist 2022).

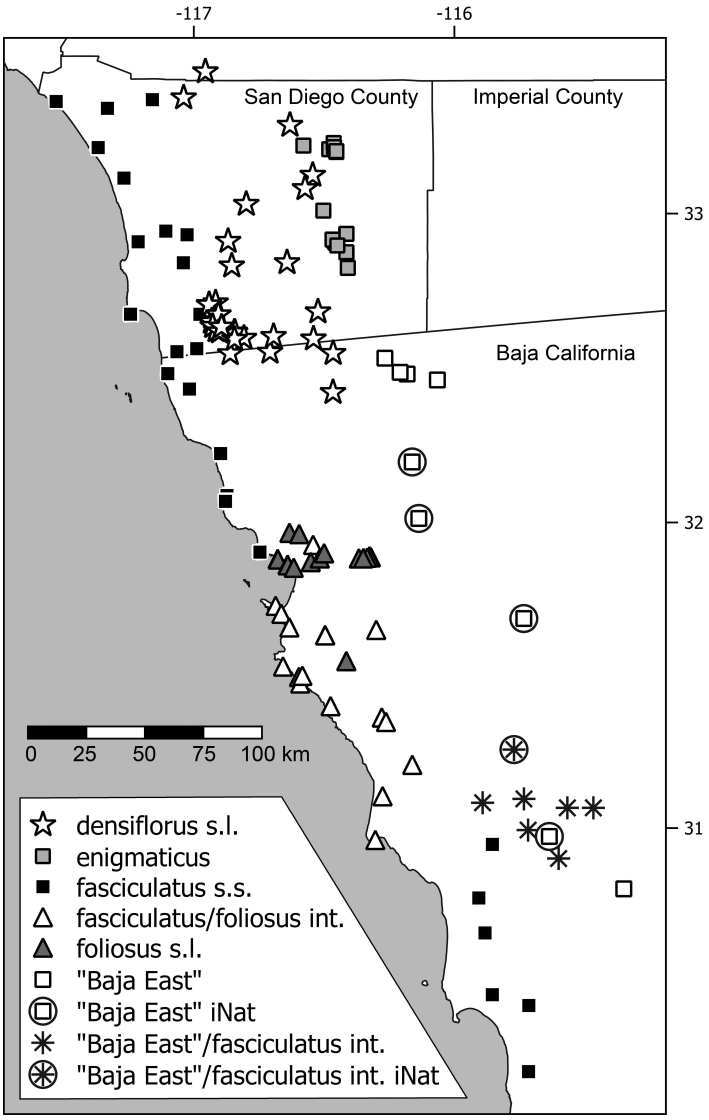

Figure 3. All *Malacothamnus* specimens measured from San Diego County and Baja California showing the full range of the three hypothesized morphological groups from Baja California (*M. fasciculatus*/*foliosus* intermediates, "Baja East", and "Baja East"/*fasciculatus* intermediates) with all nearby species. iNaturalist (iNat) observations of eastern Baja California *Malacothamnus* are included to partially fill a major specimen distribution gap and illustrate the need for further sampling in those areas.

"Baja East"/*fasciculatus* intermediates represent a geographically cohesive cluster of highly variable specimens that don't fit well with other morphological groups. They may be intermediates or hybrids between other morphological groups in the region. Alternately, they may be a single variable morphological group or extreme expressions of one or more nearby morphological groups.

To test which species the three questionable groups are most similar to, PCA was first run on all specimens of *Malacothamnus densiflorus* sensu Bates, *M. enigmaticus*, *M. fasciculatus* s.s., *M. foliosus* sensu Bates, *M. fasciculatus*/*foliosus* intermediates, "Baja East", and "Baja East"/*fasciculatus* intermediates (Fig. 4). PCA of these specimens indicates all of the ambiguous specimens (white in Fig. 4) cluster most closely with *M. fasciculatus* s.s. and *M. enigmaticus*. PC1 explains 29.9% of the variation and separates all *M. densiflorus* sensu Bates and some of *M. foliosus* sensu Bates from the ambiguous specimens. The highest-weighted characters on PC1 indicate longer stellate and glandular trichomes on both the calyx and stem, longer calyx bracts, and longer stipular bracts contributed most to negative PC1 values (Appendix 2). PC2 explains 12.3% of the variation and separates *M. foliosus* sensu Bates from the ambiguous specimens. The highest-weighted characters on PC2 indicate *M. foliosus* sensu Bates and some *M. densiflorus* sensu Bates are separated from the rest by the combination of leaf base shape, inflorescence type, calyx lobe size and shape, and/or stellate trichome length on the stem. *Malacothamnus densiflorus* sensu Bates and *M. foliosus* sensu Bates are explored further in separate sections.

A further PCA was run without *Malacothamnus densiflorus* sensu Bates and *M. foliosus* sensu Bates, which mostly separates *M. enigmaticus* from the rest on PC1 (Fig. 5). There is some overlap between *M. enigmaticus* and "Baja East" with "Baja East" appearing possibly intermediate between *M. enigmaticus* and the other morphological groups or as perhaps a morphological extreme of *M. enigmaticus*. PC1 explains 27.5% of the variation with the highest-weighted characters separating *M. enigmaticus* and "Baja East" from the rest being longer calyces, longer and wider calyx lobes, longer calyx bracts, and longer and wider stipular bracts (Appendix 2). PC2 explains 8.8% of the variation with the highest-weighted characters being stellate trichome density and leaf base shape. Sparser stellate trichomes and a tendency towards more cuneate rather than cordate leaf bases contribute most to higher PC2 values.

PCA of just *Malacothamnus enigmaticus* and "Baja East" does not show strong separation, though all "Baja East" specimens are plotted as an extreme on PC1 or PC2 just outside the cluster of *M. enigmaticus* (Fig. 6). An alternate interpretation is that the two groups are slightly separated on PC1 except for an outlier in each group. Increased sampling of "Baja East" is needed to clarify. PC1 explains 24.7% of the variation with the highest-weighted characters being calyx bract length, calyx length, calyx lobe length and width, and length of stellate trichome rays on the calyx (Appendix 2).

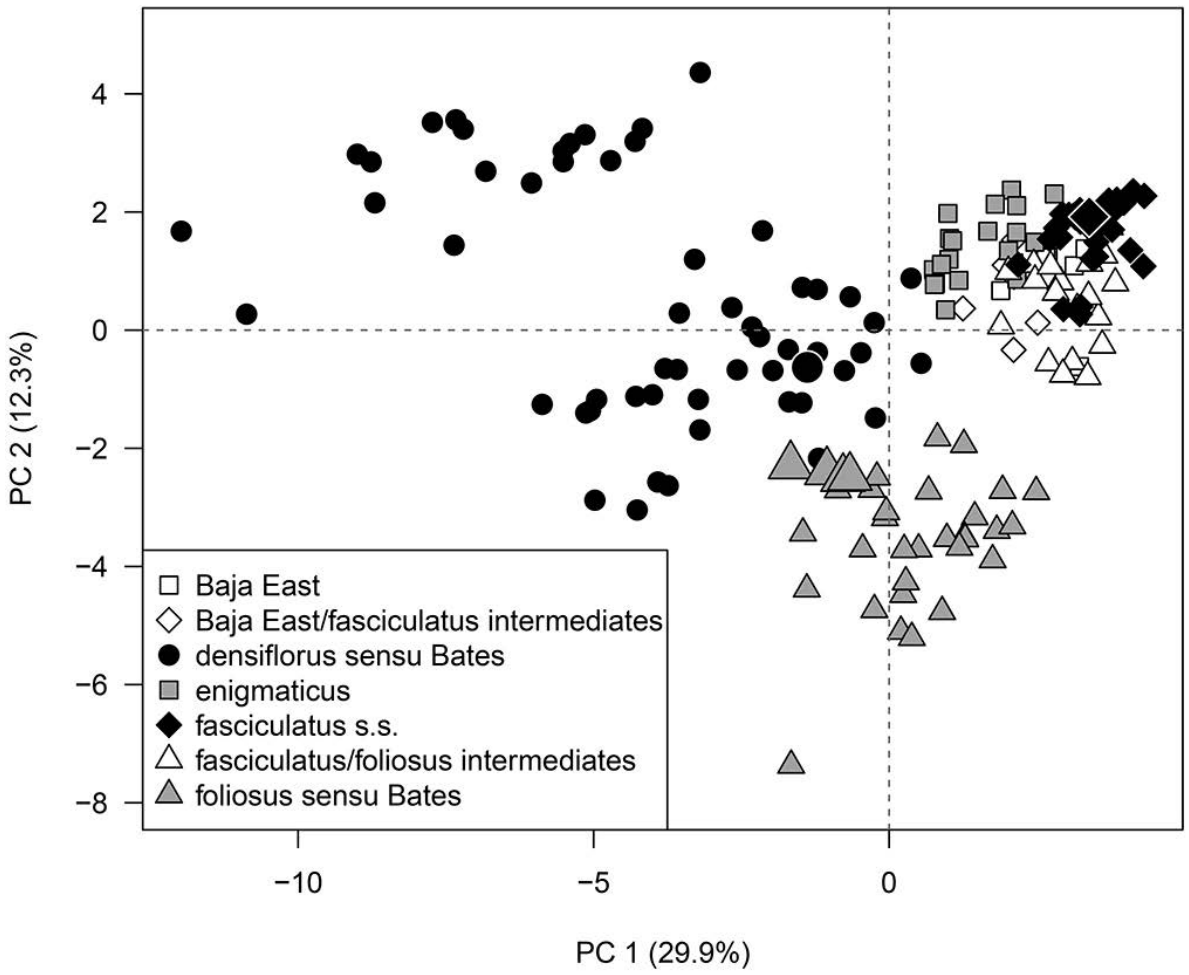

Figure 4. PCA results comparing morphology of ambiguous *Malacothamnus* specimens from Baja California to *M. densiflorus* sensu Bates, *M. enigmaticus*, *M. fasciculatus* s.s., and *M. foliosus* sensu Bates. Specimen symbols colored black and grey are relatively well-defined morphological groupings. Specimens with white symbols are those needing clarification. Larger symbols denote type specimens of *M. densiflorus*, *M. fasciculatus*, and *M. foliosus*.

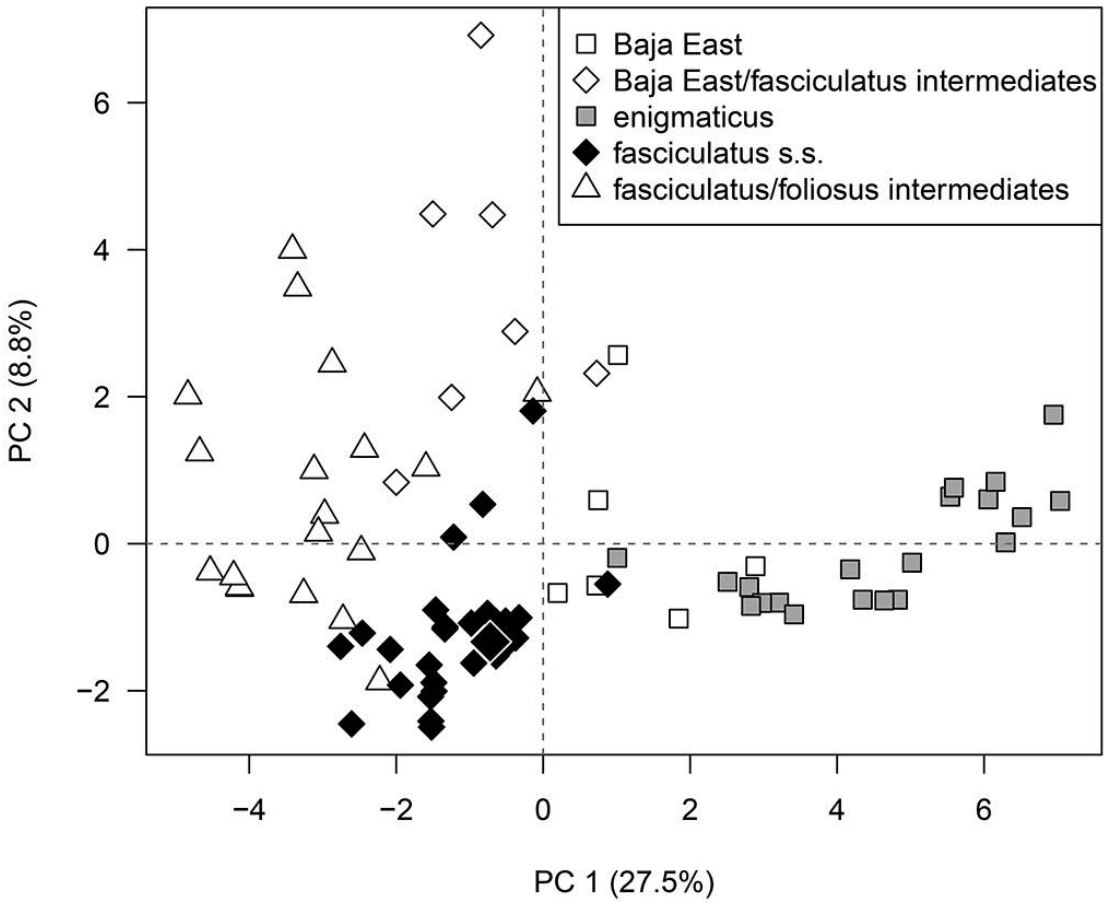

Figure 5. PCA results comparing morphology of ambiguous *Malacothamnus* specimens from Baja California *to M. fasciculatus* s.s. and *M. enigmaticus*. Square symbols represent *M. enigmaticus* and the similar "Baja East". Note both of the "Baja East" specimens with positive PC2 values are duplicate specimens, the origins of which are geographically disjunct to the south of the rest by ~225 km as seen in Fig. 3. The larger black diamond denotes the *M. fasciculatus* lectotype.

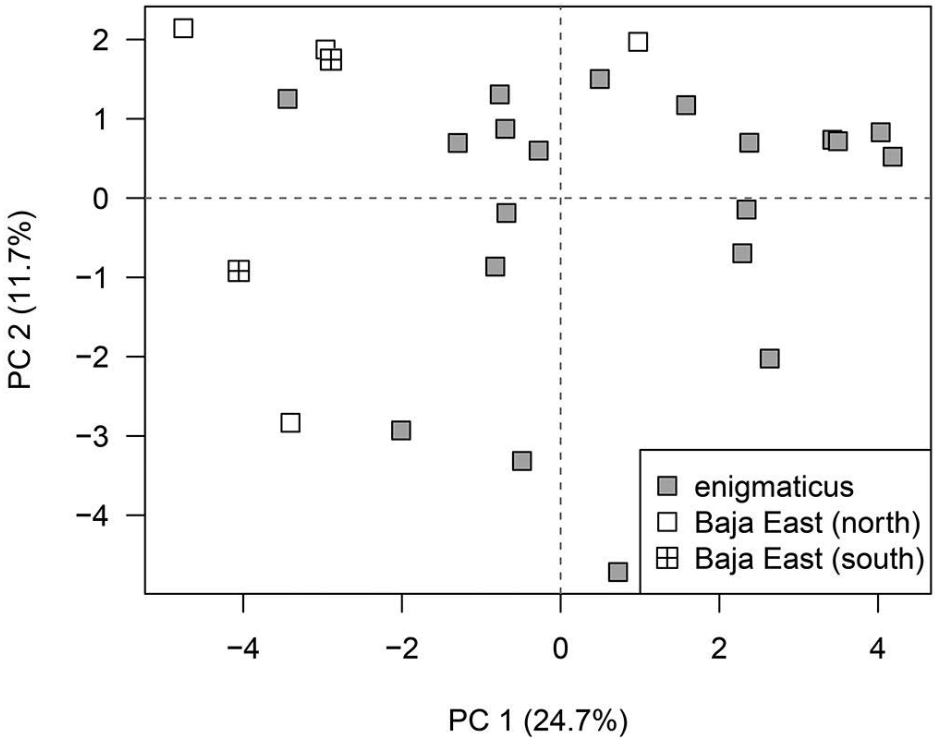

Figure 6. PCA results comparing morphology of *Malacothamnus enigmaticus* to "Baja East". "Baja East" is separated into the two sampling areas ~225 km apart as shown in Figure 3.

PCA comparing *Malacothamnus fasciculatus* s.s. with just the *M. fasciculatus*/*foliosus* intermediates and the "Baja East"/fasciculatus intermediates mostly separates the *M. fasciculatus*/*foliosus* intermediates from the "Baja East"/fasciculatus intermediates on the PC1 axis and *Malacothamnus fasciculatus* s.s. from the rest on the PC2 axis (Fig. 7). PC1 explains 15.7% of the variation with the highest-weighted characters separating the "Baja East"/fasciculatus intermediates from the *M. fasciculatus*/*foliosus* intermediates being longer calyces, calyx lobes, calyx bracts, and stellate trichome rays on the calyx (Appendix 2). PC2 explains 12.1% of the variation with the highest-weighted characters separating *M. fasciculatus* from the rest being denser stellate trichomes on the stem, calyx, and leaves; wider calyx lobes; and a tendency towards more cordate rather than cuneate leaf bases.

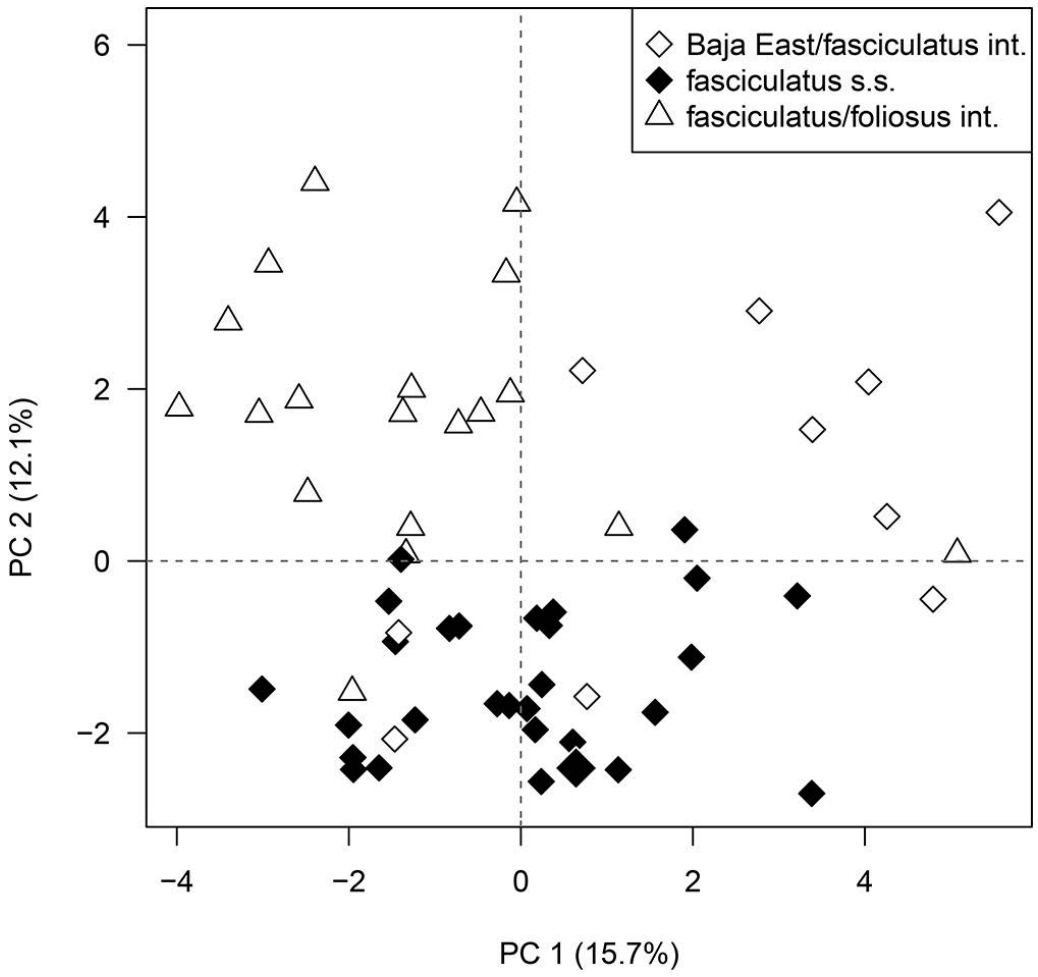

Figure 7. PCA results comparing morphology of *Malacothamnus fasciculatus* s.s. with *M. fasciculatus*/*foliosus* intermediates and "Baja East"/*fasciculatus* intermediates. The larger black diamond denotes the *M. fasciculatus* lectotype.

LDA was run on all specimens of *Malacothamnus densiflorus* sensu Bates, *M. enigmaticus*, *M. fasciculatus* s.s., *M. foliosus* sensu Bates, *M. fasciculatus*/*foliosus* intermediates, "Baja East", and "Baja East"/*fasciculatus* intermediates (Table 2). The four species groups (*M. densiflorus* sensu Bates, *M. enigmaticus*, *M. fasciculatus* s.s., and *M. foliosus* sensu Bates) were all correctly identified at least 95% of the time. "Baja east" was misclassified 50% of the time with two of the three misclassifications being assigned to the similar *M. enigmaticus*. *Malacothamnus fasciculatus*/*foliosus* intermediates were correctly classified 68% of the time and "Baja East"/*fasciculatus* intermediates were correctly classified 57% of the time. 78% of misclassifications in the two intermediate groups were assigned to the other intermediate group. A second LDA (not shown) combining "Baja east" with *M. enigmaticus* and combining the two intermediate groups yielded a 92% correct classification for each combined group.

Table 2. Predicted vs. actual group results for LDA of *Malacothamnus* specimens from San Diego County and Baja California. Blue with bold numbers indicates a correct prediction and yellow indicates an incorrect prediction.

	Predicted Group								
Actual Group	" Baja east"	" Baja east" /fasciculatus intermediates	densiflorus sensu Bates	enigmaticus	fasciculatus/foliosus intermediates	fasciculatus s.s.	foliosus sensu Bates	Total	Percent correctly identified
"Baja east"	**3**	0	0	2	0	1	0	6	50%
"Baja east"/fasciculatus intermediates	0	**4**	0	0	3	0	0	7	57%
densiflorus sensu Bates	0	1	**37**	0	1	0	0	39	95%
enigmaticus	1	0	0	**19**	0	0	0	20	95%
fasciculatus/foliosus intermediates	0	4	1	0	**13**	1	0	19	68%
fasciculatus s.s.	0	0	0	1	0	**27**	0	28	96%
foliosus sensu Bates	0	0	0	0	0	0	**34**	34	100%

PERMANOVA was run using the same set of specimens and groupings as the first LDA (Table 3). All pairwise comparisons were significant with the lowest pseudo *F*-ratios involving "Baja east" and/or the "Baja east"/fasciculatus intermediates, both of which were undersampled.

Evidence from PCAs, LDA, and PERMANOVA indicates *Malacothamnus densiflorus* sensu Bates, *M. fasciculatus* s.s., *M. foliosus* sensu Bates, and *M. enigmaticus* are morphologically distinct from each other. Considering geographic evidence as well, "Baja east"/*fasciculatus* intermediates, *fasciculatus*/*foliosus* intermediates, and "Baja east" are all reasonable hypotheses of morphological groupings, though not especially clear ones. "Baja east" clusters best with and could arguably be combined with *M. enigmaticus* but further sampling is needed to clarify this group. The "Baja east"/*fasciculatus* intermediates and *fasciculatus*/*foliosus* intermediates cluster best with *M. fasciculatus* sensu Bates. These two intermediate groups could arguably be combined into a single group but, with possible hybridization with adjacent groups involved, molecular evidence may be needed to clarify if and how both of these groups should be defined. The groups "Baja east"/*fasciculatus* intermediates and *fasciculatus*/*foliosus* intermediates are carried forward for further analysis with the more broadly classified *M. fasciculatus* sensu Bates. *Malacothamnus enigmaticus* and "Baja East" are carried forward to the full genus analyses. *Malacothamnus densiflorus* sensu Bates and *M. foliosus* sensu Bates are each further explored separately.

Table 3. PERMANOVA results from pairwise comparisons of morphological groupings of *Malacothamnus* specimens from San Diego County and Baja California ordered by pseudo *F*-ratio.

pairs	SumsOfSqs	pseudo-*F*	R^2	*p*-value
fasciculatus vs foliosus	1.17	58.1	0.49	0.001
densiflorus vs fasciculatus	1.24	47.1	0.42	0.001
densiflorus vs foliosus	1.30	46.0	0.39	0.001
enigmaticus vs foliosus	0.92	42.2	0.45	0.001
enigmaticus vs fasciculatus/foliosus intermediates	0.64	41.8	0.53	0.001
enigmaticus vs fasciculatus	0.38	31.5	0.41	0.001
densiflorus vs fasciculatus/foliosus intermediates	0.99	30.8	0.35	0.001
fasciculatus/foliosus intermediates vs foliosus	0.68	25.0	0.33	0.001
densiflorus vs enigmaticus	0.76	24.7	0.30	0.001
“Baja east”/fasciculatus intermediates vs enigmaticus	0.29	14.7	0.37	0.001
“Baja east” vs foliosus	0.36	11.9	0.24	0.001
“Baja east”/fasciculatus intermediates vs foliosus	0.35	11.5	0.23	0.001
“Baja east” vs densiflorus	0.44	10.8	0.20	0.001
fasciculatus/foliosus intermediates vs fasciculatus	0.17	9.5	0.17	0.001
“Baja east”/fasciculatus intermediates vs densiflorus	0.38	9.2	0.17	0.001
“Baja east”/fasciculatus intermediates vs fasciculatus	0.16	8.6	0.21	0.001
“Baja east” vs fasciculatus/foliosus intermediates	0.22	8.5	0.27	0.001
“Baja east” vs fasciculatus	0.11	6.7	0.17	0.002
“Baja east”/fasciculatus intermediates vs fasciculatus/foliosus intermediates	0.14	5.2	0.18	0.001
“Baja east” vs enigmaticus	0.09	4.2	0.15	0.001
“Baja east” vs “Baja east”/fasciculatus intermediates	0.12	3.2	0.23	0.001

3.2 *Malacothamnus fasciculatus* sensu Bates

Of the broad morphological groupings Bates called species, *Malacothamnus fasciculatus* sensu Bates has the broadest geographic range and includes the highest number of basionyms. With minor exceptions, this species is characterized by the combination of relatively short and narrow calyx bracts, short calyx lobes, and short and dense stellate trichomes (Bates 1963, 2015). Here, morphological groupings within *M. fasciculatus* sensu Bates plus the “Baja east”/*fasciculatus* intermediates and the *fasciculatus*/*foliosus* intermediates are assessed using PCA, LDA, and PERMANOVA to clarify finer-scale morphological groupings within *M. fasciculatus* sensu Bates.

Bates (2015) treated 12 basionyms as *Malacothamnus fasciculatus* with no infraspecific taxa (Fig. 1). Kearney (1951) treated this same group as five species, with *M. fasciculatus* having five varieties, for a total of nine taxa. Slotta (2004, 2012) chose an intermediate treatment with

the major exception of *M. arcuatus,* which she did not recognize and which she annotated the specimens of as several of Bates's species. My preliminary phylogenetic analyses, however, showed specimens of *M. arcuatus* to form a single clade with *M. hallii*, which is also included in *M. fasciculatus* sensu Bates.

Large geographic disjunctions from the mostly southern Californian and Baja Californian range of *Malacothamnus fasciculatus* sensu Bates include three northern species (*M. arcuatus*, *M. hallii*, and *M. mendocinensis*) and *Malvastrum thurberi* from southern Arizona or adjacent Mexico. Two included taxa are presumed to only occur on separate islands in the Channel Islands of California: *Malacothamnus fasciculatus* var. *catalinensis* on Santa Catalina Island and *M. f.* var. *nesioticus* on Santa Cruz Island. The basionym *Sphaeralcea fasciculata* var. *elmeri* is presumably the same as *M. hallii* which was published just five months earlier. *Malvastrum thurberi* and possibly *Malacothamnus parishii* are known only from the type collections. *Malacothamnus parishii* is presumed extinct with its purported type locality highly urbanized, though this locality is encircled by the range of *M. f.* var. *laxiflorus* and it could be an extreme form of that taxon. *Malvastrum splendens* is homotypic with *M. f.* var. *laxiflorus*. The remaining taxa associated within *M. fasciculatus* sensu Bates are *M*. *fasciculatus* s.s. and *M*. *f*. var. *nuttallii*. In addition to the basionyms associated with *M. fasciculatus* sensu Bates, Morse and Chester (2019) indicated possible undescribed taxa in Baja California that needed further sampling to resolve. These were analyzed in the previous section and the two groups "Baja east"/*fasciculatus* intermediates and *fasciculatus*/*foliosus* intermediates are carried forward here to compare to the more broadly defined *M. fasciculatus* sensu Bates.

PCA of all the named taxa within *Malacothamnus fasciculatus* sensu Bates plus the intermediate groups from Baja California separates out *M. arcuatus*, which is one of the most northern species in the group, as the most morphologically distinct relative to the rest of the group along PC1 with only minor overlap with the geographically adjacent *M. hallii* and plants from Baja California 900+ km away (Fig. 8). The primary characters contributing to the distinctness of *M. arcuatus* are both longer trichomes and longer bracts (Appendix 2). Overlap of *M. arcuatus* with intermediate specimens from Baja California is likely mostly the result of the intermediate specimens having longer trichomes due to genetic influences from the longer-trichomed *M. foliosus*. When specimens in this PCA are grouped using the three disjunct northern species (*M. arcuatus*, *M. hallii*, and *M. mendocinensis*) compared to the intermediates from Baja California and the remaining southern *M. fasciculatus* sensu Bates, the three northern species are mostly distinct from each other and from the southern specimens. Additional PCAs explore the disjunct northern and southern groups separately to clarify regional distinctions.

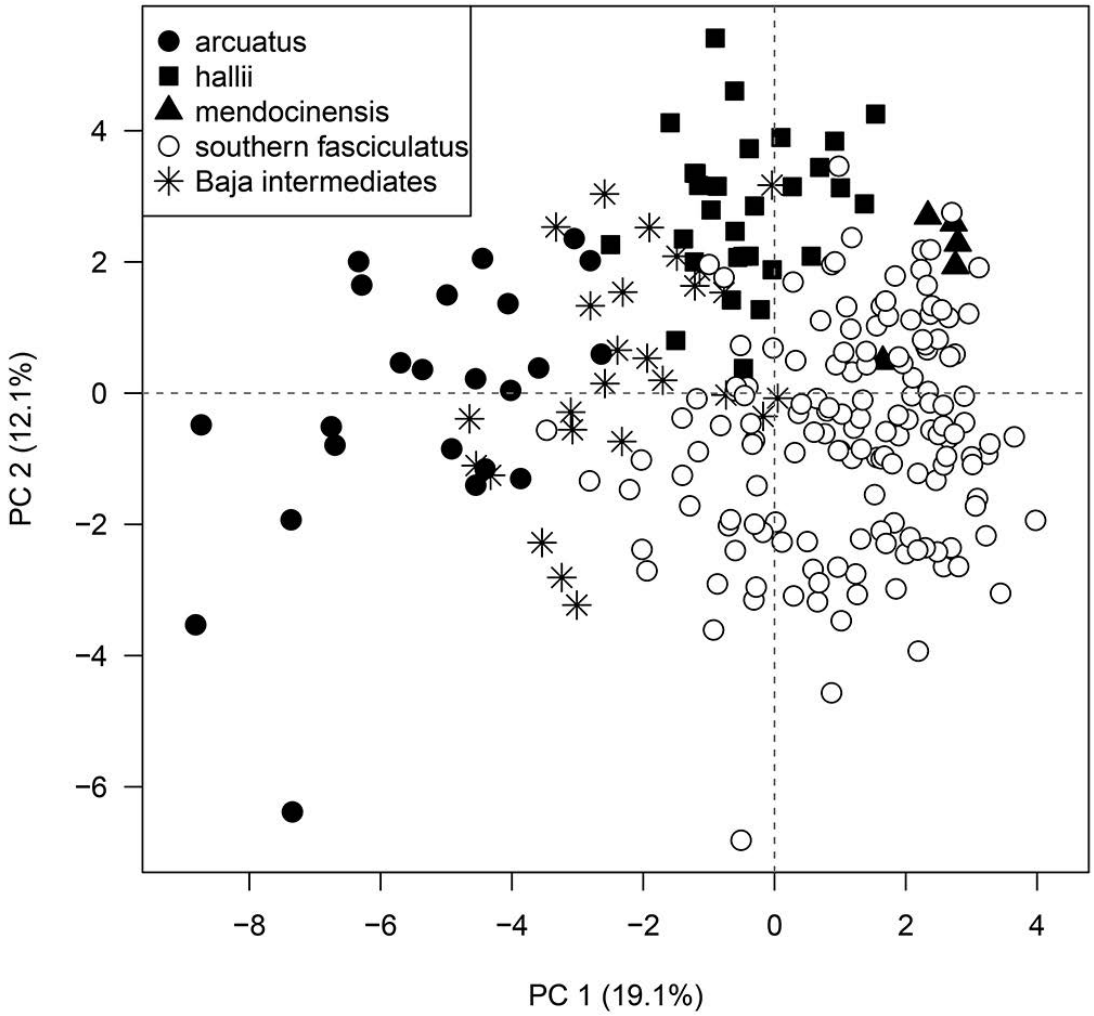

Figure 8. PCA of all groups within *Malacothamnus fasciculatus* sensu Bates including the intermediate groups from Baja California. Northern taxa are shown at the species rank as treated by Kearney. The three northern species are distinguished with black shapes, whereas the remaining southern groups of *M. fasciculatus* sensu Bates are shown as white circles with the exception that the Baja California intermediates are shown as asterisks.

PCA of the northern taxa (*Malacothamnus arcuatus*, *M. hallii*, *M. mendocinensis*, and *Sphaeralcea fasciculata* var. *elmeri*) again shows *M. arcuatus* to be largely distinct from the rest of the group on the PC1 axis with some possible *M. hallii* intermediates (Fig. 9). PC1 explains 37.3% of the variation with the highest-weighted characters being calyx length, calyx bract length, and length of stellate trichome rays on both the calyx and stem (Appendix 2). *Malacothamnus mendocinensis* separates from *M. hallii* on PC2, which explains 9.7% of the variation with calyx lobe size, calyx bract color, and leaf base shape being the highest-weighted characters. The fact that both the *M. hallii* and *S. f.* var. *elmeri* types plot close together and that they are both from Mount Diablo in Contra Costa County, CA indicates *S. f.* var. *elmeri* has been correctly treated as a synonym of *M. hallii*. *Malacothamnus arcuatus*, *M. hallii*, and *M. mendocinensis* can be mostly distinguished based on two characters measured: calyx bract length and mean length of stellate trichome rays on the stem (Fig. 10). The lectotype of *M.*

arcuatus (UC191563) was not available to fully measure, however, a digital scan of the specimen was examined, and it clearly fits with the unambiguous *M. arcuatus* specimens measured as it has calyx bracts averaging ~5 mm and many stellate trichome rays on the stem appearing to be ~0.5 mm or greater. *Malacothamnus arcuatus* and *M. hallii* are geographically adjacent and likely intergrade. *Malacothamnus mendocinensis* is disjunct from the other two species by ~210 km and has only been documented in two locations. The gap seen in *M. mendocinensis* in the PCA plot corresponds to a geographic gap between the two known locations of this species. This gap would presumably close with further sampling if other populations are ever discovered.

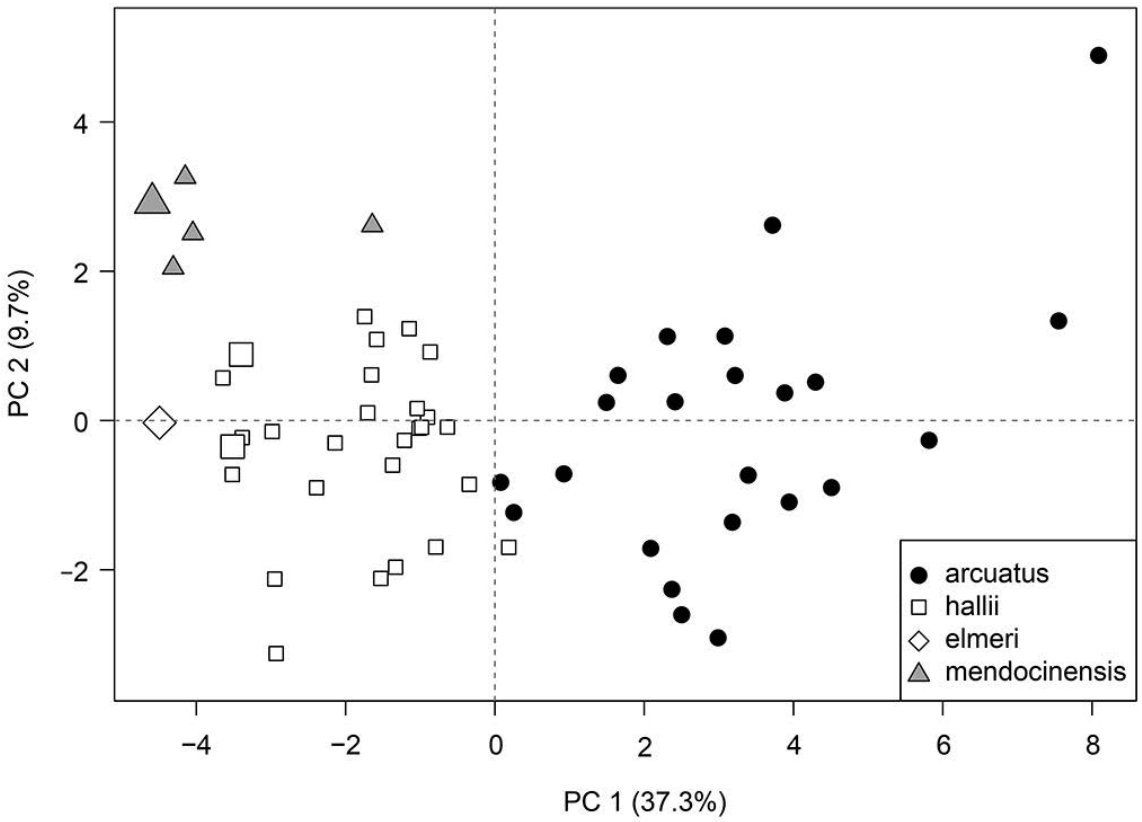

Figure 9. PCA results comparing morphology of northern taxa within *Malacothamnus fasciculatus* sensu Bates. Larger symbols denote type specimens. The lectotype of *M. arcuatus* was unavailable for measuring.

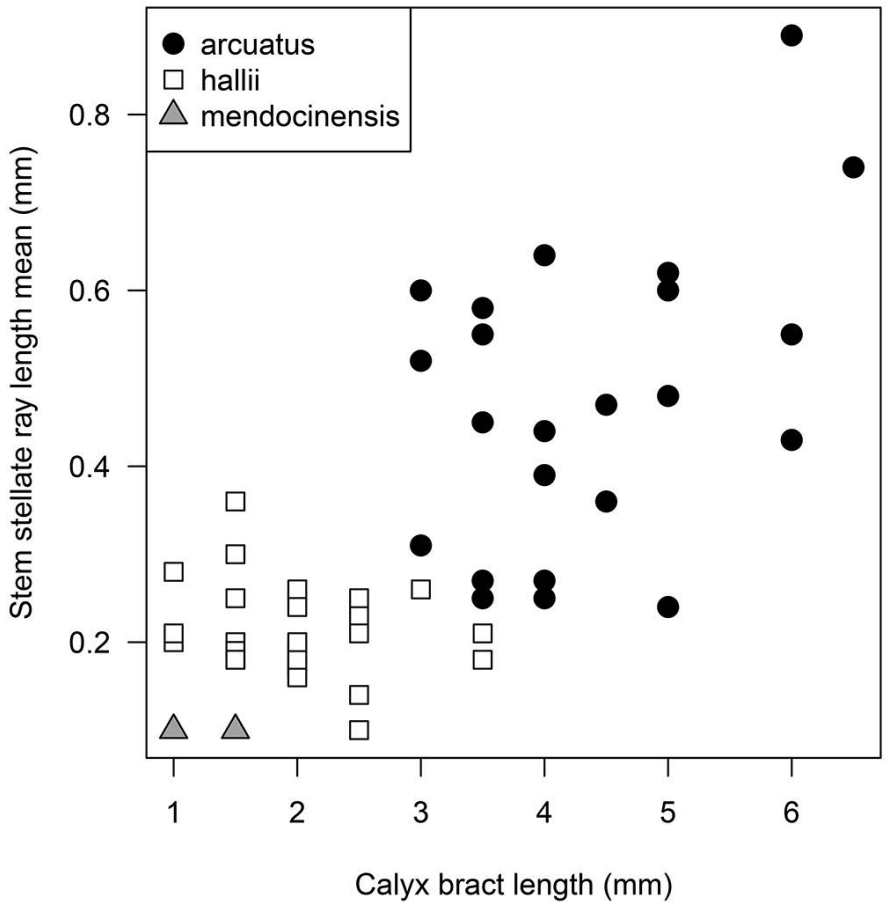

Figure 10. Scatterplot showing the utility of the combination of calyx bract length and length of stellate trichome rays on the stem in distinguishing *Malacothamnus arcuatus*, *M. hallii*, and *M. mendocinensis*. Note that *M. arcuatus* and *M. hallii* likely intergrade where their ranges come together.

PCA of all the southern taxa within *Malacothamnus fasciculatus* sensu Bates, including the Baja California intermediates (Fig. 11), shows the Baja California intermediates to be most similar to *M. fasciculatus* s.s., which they were analyzed with in the previous section. In this PCA, *Malvastrum thurberi*, which is only known from its disjunct type collection purportedly near the border of Arizona and Mexico and which is generally recognized as a synonym of *M. fasciculatus* s.s., indeed plots with *M. fasciculatus* s.s. In another PCA including just *Malvastrum thurberi*, *M. fasciculatus* s.s., and the Baja California intermediates (Fig. 12), it was verified that *Malvastrum thurberi* again clusters with *M. fasciculatus* s.s.

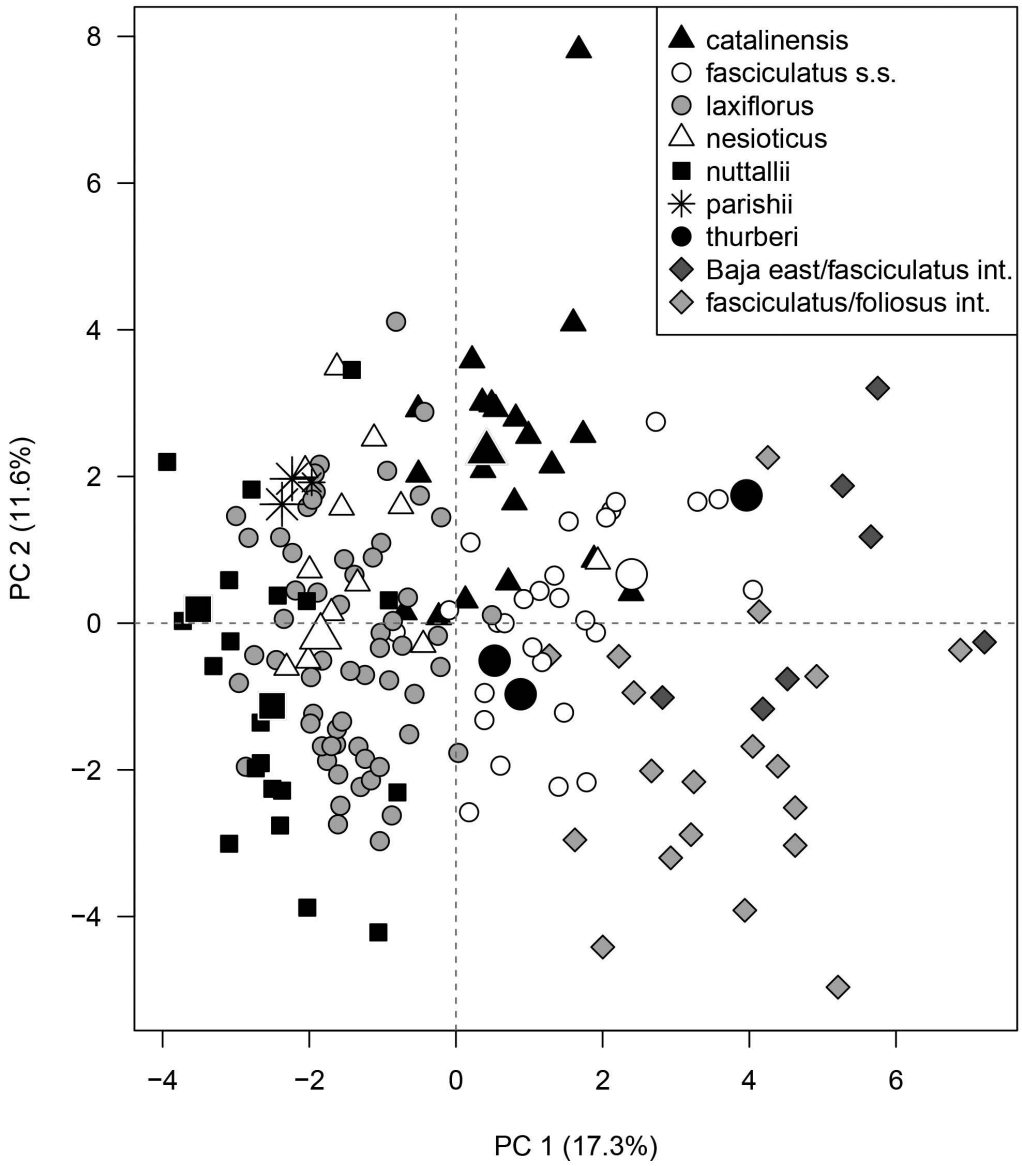

Figure 11. PCA results comparing morphology of southern taxa within *Malacothamnus fasciculatus* sensu Bates including Baja California intermediates. Diamonds denote Baja California intermediates and triangles denote island endemics. Larger symbols denote type specimens. The neotype of *M. f.* var. *laxiflorus* was not measured.

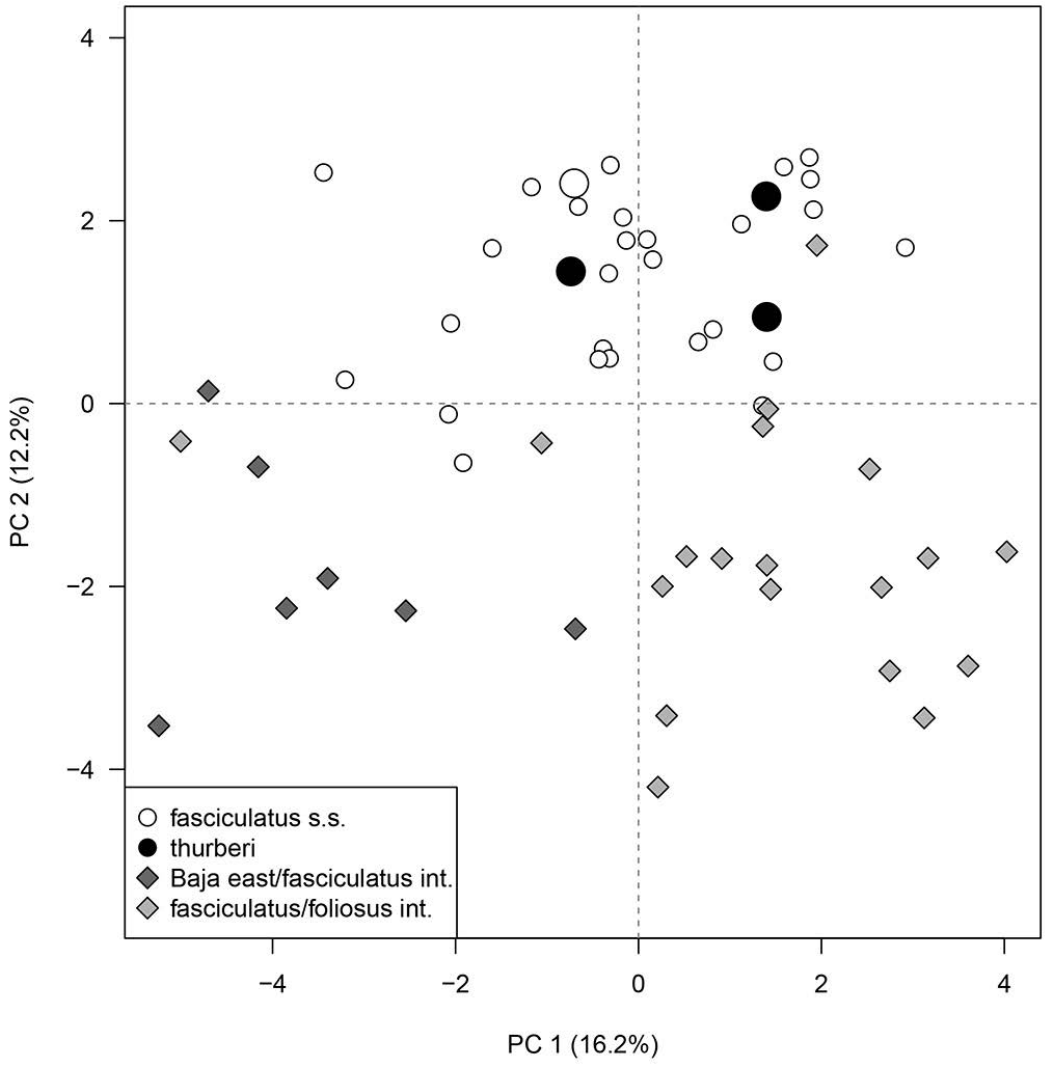

Figure 12. PCA results comparing morphology of *Malvastrum thurberi* to *Malacothamnus fasciculatus* s.s. and Baja California intermediates. Larger symbols denote type specimens.

PCA of all the southern taxa within *Malacothamnus fasciculatus* sensu Bates excluding the Baja California intermediates (Fig. 13) shows discernible patterns based on taxon assignment, however, all taxa overlap with others to some extent. PC1 mostly divides *M. fasciculatus* s.s. and *M. f.* var. *catalinensis* from *M. f.* var. *laxiflorus, M. f.* var*. nesioticus,* and *M. f.* var*. nuttallii*. PC2 mostly divides *M. fasciculatus* s.s. from *M. f.* var. *catalinensis*. *Malvastrum thurberi* again clusters with *Malacothamnus fasciculatus* s.s.

Further exploring taxa with more positive PC1 values in Fig. 13, PCA of *M. fasciculatus* s.s*., M. f.* var. *catalinensis*, and *Malvastrum thurberi* increases separation of *M. fasciculatus* s.s*.* and *M. f.* var. *catalinensis* (Fig. 14). PCA of just *M. fasciculatus s.s.* and the disjunct *Malvastrum thurberi* (Fig. 15) follows Fig. 14 indicating no separation of *M. fasciculatus s.s.* and *Malvastrum thurberi,* which supports previous treatments recognizing *Malvastrum thurberi* as a synonym of *M. fasciculatus* s.s.

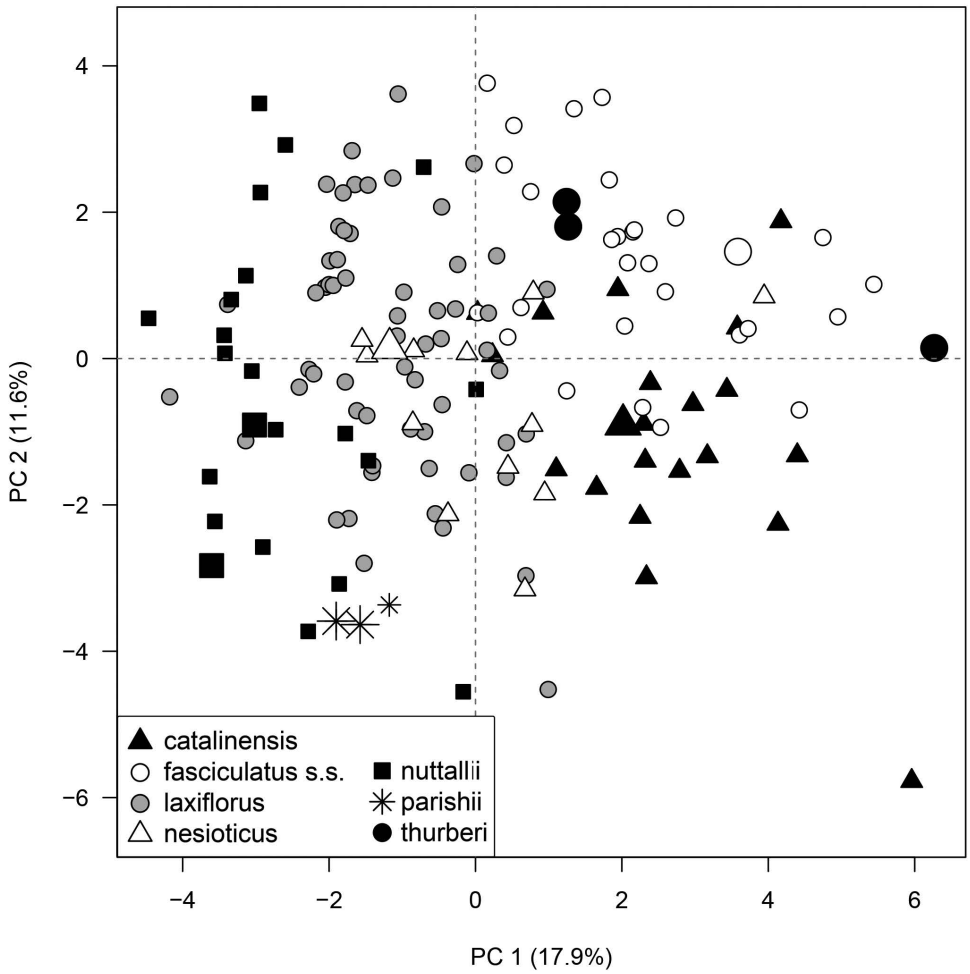

Figure 13. PCA results comparing morphology of southern taxa within *Malacothamnus fasciculatus* sensu Bates excluding Baja California intermediates. Triangles denote island endemics. Larger symbols denote type specimens. The neotype of *M. f.* var. *laxiflorus* was not measured.

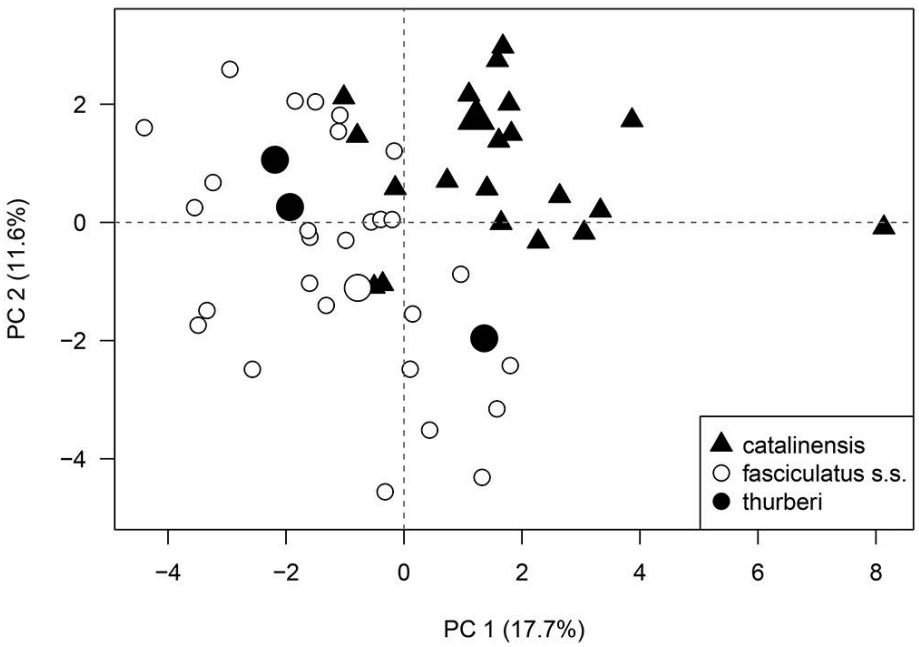

Figure 14. PCA results comparing morphology of *Malacothamnus fasciculatus* s.s.*, M. f.* var. *catalinensis*, and *Malvastrum thurberi.* Larger symbols denote type specimens.

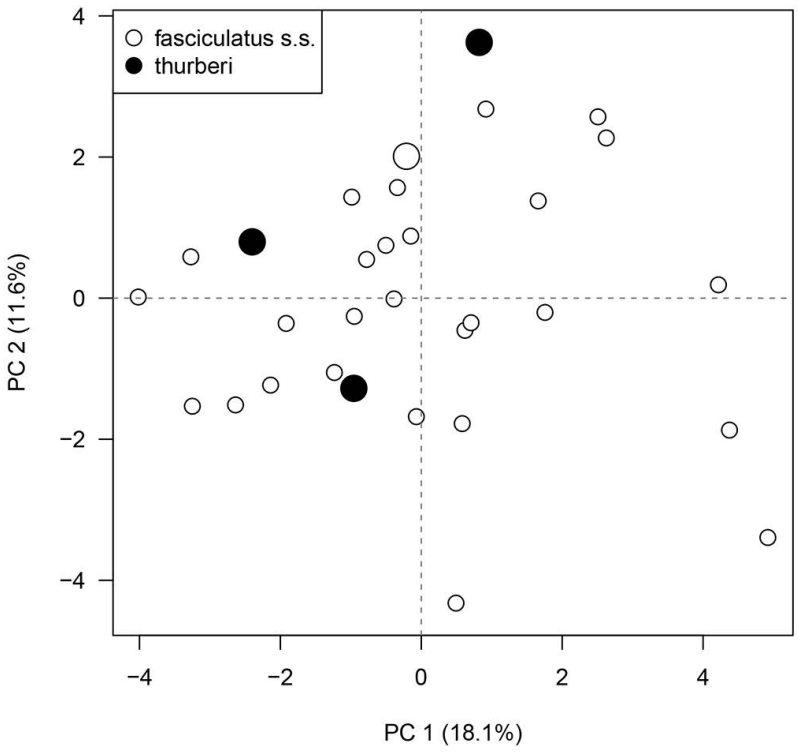

Figure 15. PCA results comparing morphology of *Malvastrum thurberi* to *Malacothamnus fasciculatus* s.s.. Larger symbols denote type specimens.

Further exploring taxa with generally negative PC1 values in Fig. 13, PCA of *M. f.* var. *laxiflorus*, *M. f*. var. *nesioticus*, *M. f*. var. *nuttallii*, and *M. parishii* (Fig. 16) does not show any as distinct. PCA of *M. f.* var. *laxiflorus*, *M. f*. var. *nuttallii*, and *M. parishii* (Fig. 17) mostly separates *M. f.* var. *laxiflorus* vs. *M. f*. var. *nuttallii*, though there is no clear line between groups in the PCA and two major outliers of *M. f.* var*. nuttallii* are plotted within the distribution of *M. f.* var*. laxiflorus* on these axes. One major outlier is possibly intermediate between *M. f*. var. *nuttallii* and *M. orbiculatus* while the other, mostly similar to *M. f*. var. *nuttallii*, has abnormally sparse leaf trichomes. Despite overlap in the PCA, *M. f.* var. *nuttallii* is geographically separated from *M. f.* var. *laxiflorus* by ~30 km, has a peak flowering time about one month later than nearby *M. f.* var. *laxiflorus,* and is generally easily identified by its much denser and smaller trichomes on the adaxial side of the leaf. Only two locations of iNaturalist observations within the range of *M. f.* var. *nuttallii* appear to fit another variety of *M. fasciculatus* and these were likely introduced via a habitat restoration project due to misidentification or to using a taxonomic treatment that did not recognize the varieties of *M. fasciculatus*. Also of note are two specimens of *M. f.* var. *laxiflorus* from the Santa Rosa Mountains in Riverside County, CA that are outliers on PC1. PCA of *M. f.* var. *laxiflorus*, *M. f*. var. *nesioticus*, and *M. parishii* again shows clustering by taxon with some overlap and the Santa Rosa Mountains specimens as outliers (Fig. 18).

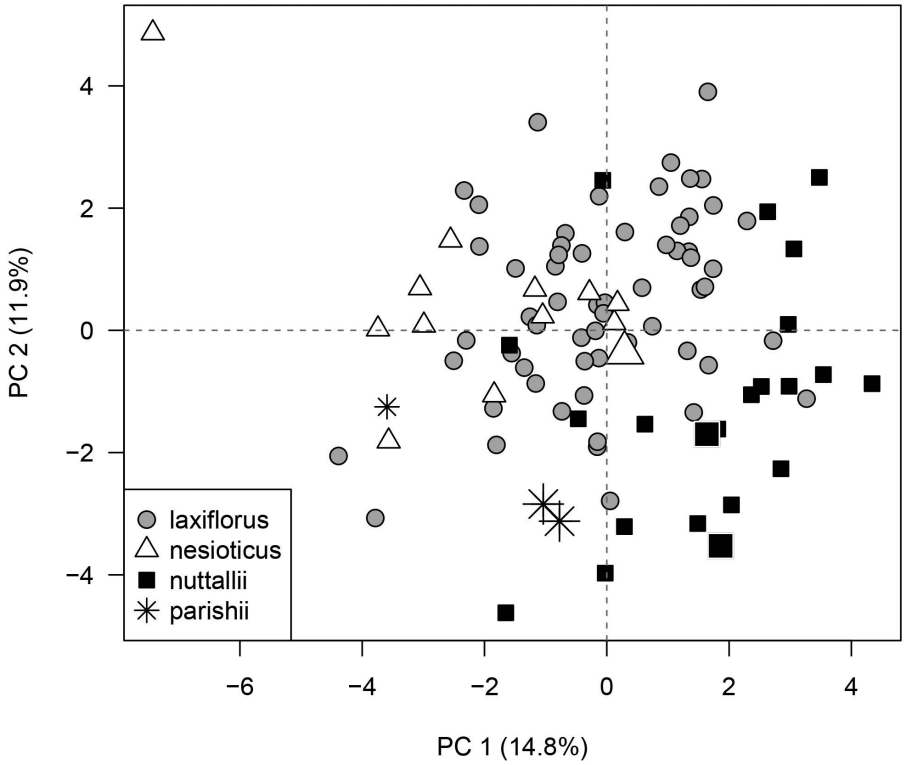

Figure 16. PCA results comparing morphology of *M. fasciculatus* var. *laxiflorus*, *M. f*. var. *nesioticus*, *M. f*. var. *nuttallii*, and *M. parishii*. Larger symbols denote type specimens. The neotype of *M. f.* var. *laxiflorus* was not measured.

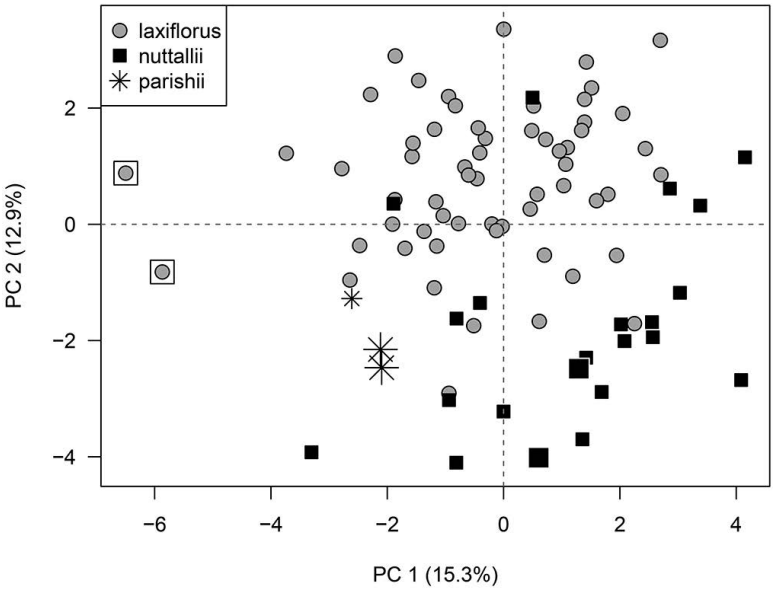

Figure 17. PCA results comparing morphology of *Malacothamnus fasciculatus* var. *laxiflorus, M. f.* var. *nuttallii*, and *M. parishii.* Larger symbols denote type specimens. The neotype of *M. f.* var. *laxiflorus* was not measured. White squares around *M. f.* var. *laxiflorus* symbols denote specimens from the Santa Rosa Mountains.

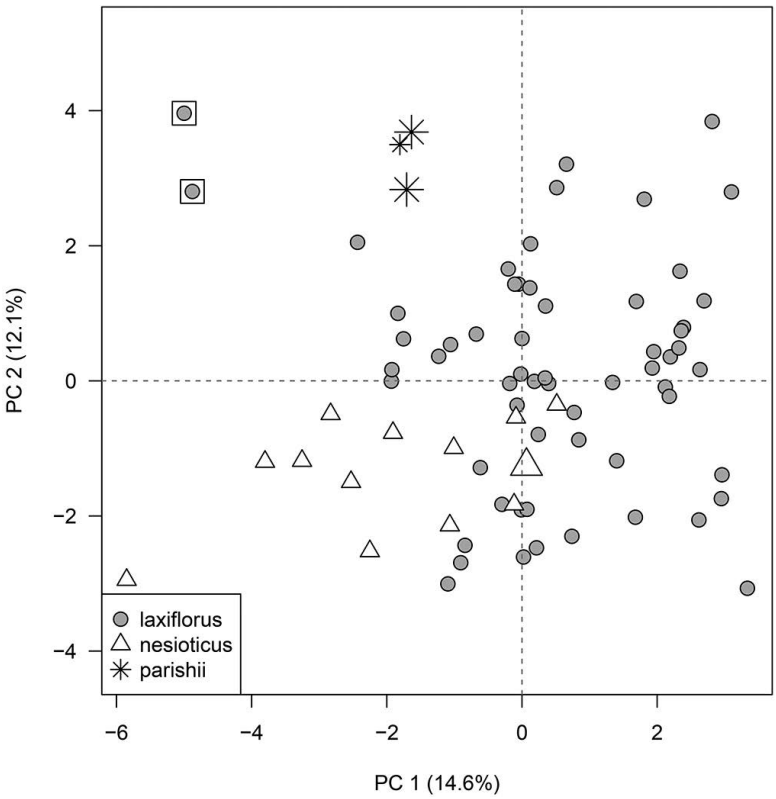

Figure 18. PCA results comparing morphology of *Malacothamnus fasciculatus* var. *laxiflorus, M. f.* var. *nesioticus*, and *M. parishii.* Larger symbols denote type specimens. The neotype of *M. f.* var. *laxiflorus* was not measured. White squares around *M. f.* var. *laxiflorus* symbols denote specimens from the Santa Rosa Mountains.

From the standpoint of grouping specimens as taxon hypotheses for DNA analyses, *M. f.* var. *catalinensis*, *M. f*. var. *nesioticus*, and *M. f*. var. *nuttallii* are all geographically isolated groups. There is, however, no clear geographic boundary between *M. fasciculatus* s.s. and *M. f.* var. *laxiflorus*. Kearney (1951) notes these two taxa are quite distinct in their extreme forms, but that intergradation is complete. PCA of *M. fasciculatus s.s., M. f.* var. *laxiflorus,* and *M. parishii,* with a geographic boundary between *M. fasciculatus* s.s. and *M. f.* var. *laxiflorus* mostly drawn near the northern border of San Diego County, divides *M. fasciculatus* s.s. and *M. f.* var. *laxiflorus* into relatively clear clusters along PC1 but with some overlap (Fig. 19).

The two Santa Rosa Mountains specimens of *M. f.* var. *laxiflorus* are again outliers. Both the morphology and collection location of the Santa Rosa Mountains specimens suggest they may be intermediate with *M. enigmaticus* and/or *M. densiflorus*.

The two type specimens of *M. parishii*, and the only other specimen I found to fit well with them, consistently plot near the outer edge of the *M. f.* var. *laxiflorus* PCA cluster. While this could indicate that *M. parishii* is an extreme form of *M. f.* var. *laxiflorus*, it may also indicate that *M. parishii* is a similar but distinct taxon. *Malacothamnus parishii* is distinguished from *M. f.* var. *laxiflorus* in this study by the combination of leaf base shape and calyx length, though additional sampling of *M. parishii* would be useful if another population of this presumed extinct species is ever found. All leaves on the specimens of *M. parishii* have cuneate bases whereas *M. f.* var. *laxiflorus* may have some leaves with cuneate bases but always has some that are cordate and/or truncate as well. As the specimens measured represent only the distal portion of the stem, truncate and/or cordate leaves could possibly be found more proximally on the stems of *M. parishii*. However, the *M. parishii* isotype P02286284 (digital image examined) has ~12 nodes with leaves below the inflorescence on which all the leaves are at least slightly cuneate at the base. The calyces of *M. parishii* measured for analysis were all 9 mm long, whereas *M. f.* var. *laxiflorus* was generally ≤ 8.5 mm, however, ~5% of *M. f.* var. *laxiflorus* measured 9–9.5 mm. Additional *M. parishii* calyces measured, including those from scanned images of the remaining type specimens, range from 8–10 mm long with most around 9 mm.

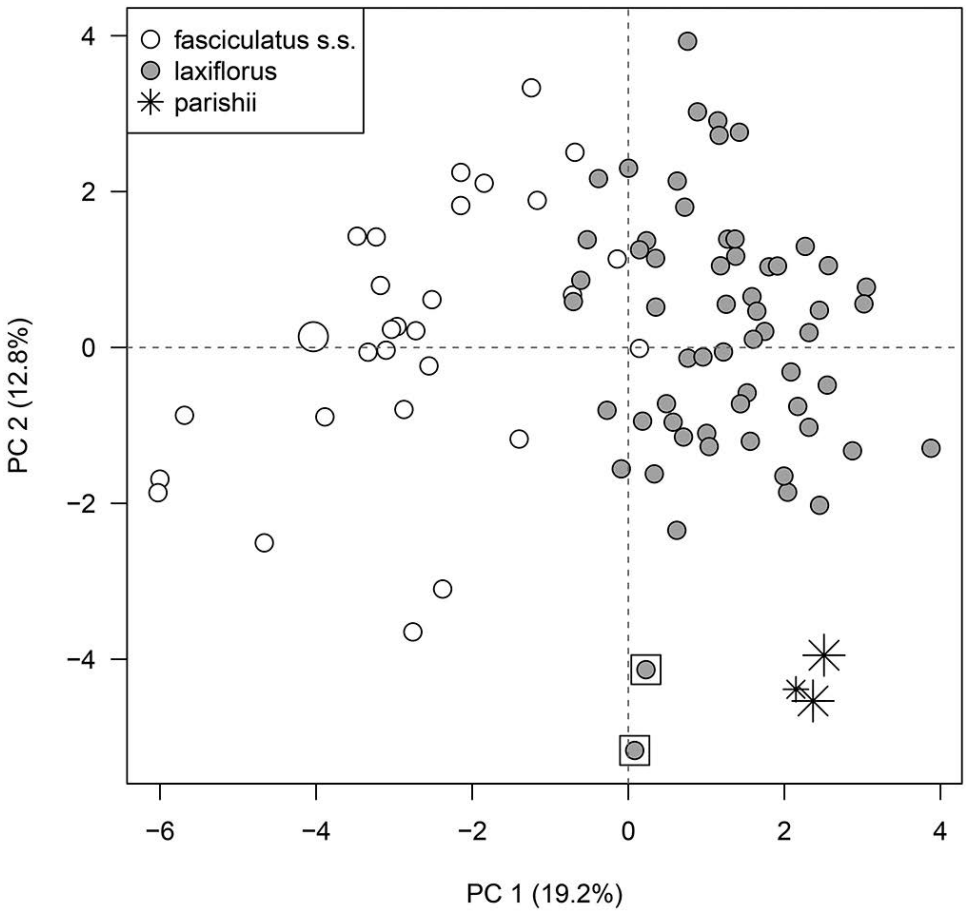

Figure 19. PCA results comparing morphology of *Malacothamnus fasciculatus* var. *laxiflorus, M. fasciculatus* s.s., and *M. parishii.* Larger symbols denote type specimens. The neotype of *M. f.* var. *laxiflorus* was not measured. Squares around *M. f.* var. *laxiflorus* symbols denote specimens from the Santa Rosa Mountains.

PCAs indicate that all the taxa within *M. fasciculatus* sensu Bates as treated by Kearney (Fig. 1) form both morphological and geographic groupings that are plausible taxon hypotheses. Also following Kearney's treatment, *Malvastrum thurberi* appears to be correctly treated as a synonym of *M. fasciculatus* s.s. and *Sphaeralcea fasciculata* var. *elmeri* appears to be correctly treated as synonym of *M. hallii*. However, as *Malvastrum thurberi* is geographically disjunct and sampling for this study is limited to the type specimens, it should be further investigated if new plants are ever found near the purported type locality. In addition, PCAs indicated two possible hybrid groupings in Baja California as well as a third in the Santa Rosa Mountains of Riverside County, CA. Geographic distribution of PCA-based morphological groupings in *M. fasciculatus* sensu Bates, excluding the disjunct *Malvastrum thurberi* type locality, are shown in Fig. 20 and Fig. 21.

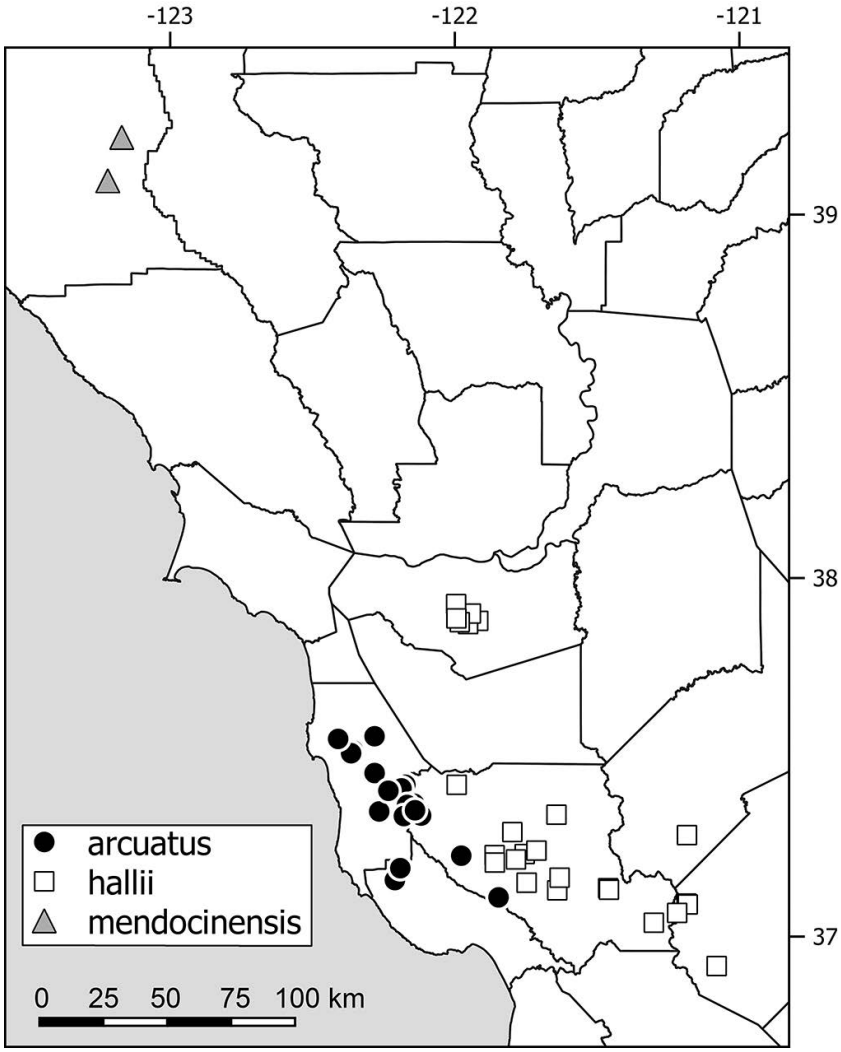

Figure 20. Map of northern *Malacothamnus fasciculatus* sensu Bates specimens measured classified by PCA resolved groupings. Black lines indicate boundaries of California counties.

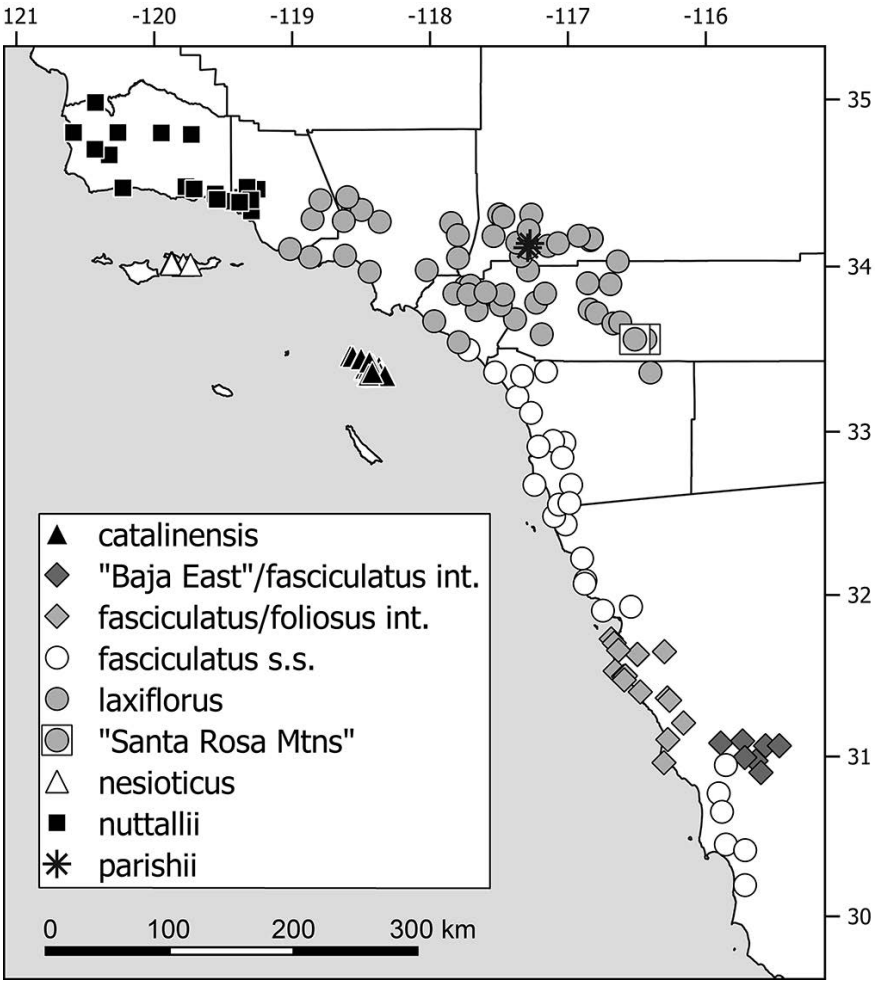

Figure 21. Map of southern *Malacothamnus fasciculatus* sensu Bates specimens measured classified by PCA resolved groupings excluding the highly disjunct type locality of *Malvastrum thurberi*. Black lines indicate boundaries of California counties and Baja California.

LDA of *Malacothamnus fasciculatus* sensu Bates using the taxa of Kearney plus the three possible hybrid groups yields greater than 75% correct classification for all of Kearney's taxa (Table 4). Misclassifications for these morphological groups were mostly as expected based on overlap between groups in PCAs. The two groups with the lowest percent of correct classifications were groups of possible hybrids. The *M. fasciculatus*/*foliosus* intermediates had only 63% correct classification with six of the seven misclassifications in that group being with the geographically adjacent groups they may arguably belong to. The Santa Rosa group, which is likely of hybrid origin with or an extreme form of *M. f.* var. *laxiflorus*, only had two specimens measured with one misclassified as *M. f.* var. *laxiflorus*.

PERMANOVA was run using the same specimens and groupings as the LDA (Table 5). All but six pairwise comparisons were significant. The six comparisons found insignificant each involve the three *M. parishii* specimens and/or the two Santa Rosa Mountains specimens. The small sample size of these groups may not have been adequate to test for significant differences between these and morphologically similar groups.

Table 4. Predicted vs. actual group results of LDA comparing taxa of Kearney plus the three possible hybrid groups within *Malacothamnus fasciculatus* sensu Bates. Blue with bold numbers indicates a correct prediction and yellow indicates an incorrect prediction.

	Predicted Group													
Actual Group	arcuatus	" Baja east" /fasciculatus intermediates	catalinensis	fasciculatus/foliosus intermediates	Fasciculatus s.s.	hallii	laxiflorus	mendocinensis	nesioticus	nuttallii	parishii	" Santa Rosa"	Total	Percent correctly identified
arcuatus	**22**	0	0	0	0	0	0	0	0	0	1	0	23	97%
"Baja east"/fasciculatus intermediates	0	**6**	0	1	0	0	0	0	0	0	0	0	7	86%
catalinensis	0	0	**18**	0	2	0	0	0	1	0	0	0	21	86%
fasciculatus/foliosus intermediates	1	2	0	**12**	4	0	0	0	0	0	0	0	20	63%
fasciculatus s.s.	0	0	2	1	**27**	1	1	0	0	0	0	0	32	84%
hallii	1	0	0	0	0	**27**	0	0	0	1	0	0	29	93%
laxiflorus	0	0	2	0	1	0	**49**	1	1	3	0	1	58	85%
mendocinensis	0	0	0	0	0	0	1	**4**	0	0	0	0	5	80%
nesioticus	0	0	0	0	0	0	2	0	**10**	1	0	0	13	77%
nuttallii	0	0	0	0	0	0	4	0	0	**18**	0	0	22	82%
parishii	0	0	0	0	0	0	0	0	0	0	**3**	0	3	100%
"Santa Rosa"	0	0	0	0	0	0	1	0	0	0	0	**1**	2	50%

Table 5. PERMANOVA results from pairwise comparisons of morphological groups in *Malacothamnus fasciculatus* sensu Bates ordered by pseudo *F*-ratio. Insignificant *p*-values are in bold.

pairs	SumsOfSqs	pseudo-*F*	R^2	*p*-value
arcuatus vs laxiflorus	1.11	72.4	0.48	0.001
arcuatus vs nuttallii	0.92	49.8	0.54	0.001
arcuatus vs nesioticus	0.76	43.2	0.56	0.001
arcuatus vs catalinensis	0.65	38.0	0.48	0.001
catalinensis vs hallii	0.68	36.5	0.43	0.001
hallii vs laxiflorus	0.62	34.8	0.29	0.001
fasciculatus s.s. vs nuttallii	0.63	34.4	0.40	0.001
arcuatus vs fasciculatus s.s.	0.56	31.6	0.37	0.001
hallii vs nuttallii	0.54	29.4	0.37	0.001
fasciculatus/foliosus intermediates vs nuttallii	0.76	27.5	0.41	0.001

pairs	SumsOfSqs	pseudo-*F*	R^2	*p*-value
arcuatus vs hallii	0.47	27.2	0.35	0.001
fasciculatus/foliosus intermediates vs laxiflorus	0.58	26.9	0.26	0.001
catalinensis vs nuttallii	0.47	25.2	0.38	0.001
hallii vs nesioticus	0.51	25.1	0.39	0.001
"Baja east"/fasciculatus intermediates vs nuttallii	0.66	25.0	0.48	0.001
"Baja east"/fasciculatus intermediates vs laxiflorus	0.50	24.1	0.28	0.001
fasciculatus s.s. vs hallii	0.46	23.8	0.29	0.001
catalinensis vs laxiflorus	0.37	22.8	0.23	0.001
arcuatus vs mendocinensis	0.42	21.2	0.45	0.001
fasciculatus s.s. vs laxiflorus	0.33	20.3	0.19	0.001
catalinensis vs fasciculatus/foliosus intermediates	0.49	20.0	0.35	0.001
"Baja east"/fasciculatus intermediates vs nesioticus	0.53	19.5	0.52	0.001
arcuatus vs fasciculatus/foliosus intermediates	0.49	18.7	0.32	0.001
fasciculatus/foliosus intermediates vs nesioticus	0.48	17.1	0.36	0.001
mendocinensis vs parishii	0.31	16.7	0.74	**0.019**
fasciculatus/foliosus intermediates vs hallii	0.38	15.9	0.26	0.001
"Baja east"/fasciculatus intermediates vs hallii	0.40	15.0	0.31	0.001
fasciculatus s.s. vs nesioticus	0.30	14.5	0.25	0.001
"Baja east"/fasciculatus intermediates vs catalinensis	0.37	13.7	0.34	0.001
catalinensis vs mendocinensis	0.26	12.4	0.34	0.001
arcuatus vs parishii	0.27	12.1	0.34	0.001
laxiflorus vs nuttallii	0.27	12.1	0.13	0.001
nesioticus vs nuttallii	0.24	11.3	0.26	0.001
"Baja east"/fasciculatus intermediates vs mendocinensis	0.44	11.3	0.53	0.004
catalinensis vs parishii	0.25	10.7	0.33	0.004
arcuatus vs "Baja east"/fasciculatus intermediates	0.29	10.4	0.27	0.001
fasciculatus s.s. vs parishii	0.23	10.3	0.24	0.001
hallii vs parishii	0.22	10.2	0.25	0.002
fasciculatus/foliosus intermediates vs fasciculatus s.s.	0.26	10.1	0.17	0.001
catalinensis vs fasciculatus s.s.	0.20	10.0	0.16	0.001
fasciculatus/foliosus intermediates vs parishii	0.36	9.8	0.33	0.001
arcuatus vs "Santa Rosa"	0.24	9.7	0.30	0.006
mendocinensis vs nesioticus	0.18	9.3	0.37	0.001
fasciculatus/foliosus intermediates vs mendocinensis	0.32	9.0	0.29	0.001
hallii vs "Santa Rosa"	0.20	9.0	0.24	0.002
"Baja east"/fasciculatus intermediates vs fasciculatus s.s.	0.23	8.9	0.19	0.001

pairs	SumsOfSqs	pseudo-*F*	R^2	*p*-value
fasciculatus s.s. vs mendocinensis	0.19	8.5	0.20	0.001
hallii vs mendocinensis	0.21	8.4	0.21	0.001
mendocinensis vs "Santa Rosa"	0.17	8.2	0.62	**0.050**
"Baja east"/fasciculatus intermediates vs parishii	0.34	8.0	0.50	**0.014**
laxiflorus vs nesioticus	0.15	7.8	0.10	0.001
nuttallii vs "Santa Rosa"	0.20	7.4	0.25	0.005
nesioticus vs parishii	0.18	7.2	0.34	0.001
catalinensis vs nesioticus	0.16	6.9	0.18	0.001
nuttallii vs parishii	0.19	6.7	0.23	0.002
nesioticus vs "Santa Rosa"	0.14	5.6	0.30	**0.014**
laxiflorus vs parishii	0.13	5.3	0.08	0.001
"Baja east"/fasciculatus intermediates vs fasciculatus/foliosus intermediates	0.19	5.2	0.18	0.001
fasciculatus/foliosus intermediates vs "Santa Rosa"	0.21	5.2	0.21	0.007
mendocinensis vs nuttallii	0.12	4.5	0.15	0.001
catalinensis vs "Santa Rosa"	0.11	4.5	0.18	0.008
laxiflorus vs "Santa Rosa"	0.09	4.0	0.07	0.002
fasciculatus s.s. vs "Santa Rosa"	0.09	4.0	0.11	0.002
parishii vs "Santa Rosa"	0.16	4.0	0.57	**0.100**
"Baja east"/fasciculatus intermediates vs "Santa Rosa"	0.19	3.7	0.35	**0.025**
laxiflorus vs mendocinensis	0.08	3.2	0.05	0.004

Evidence from PCAs, LDA, and PERMANOVA supports all taxa within *M. fasciculatus* sensu Bates as recognized by Kearney, plus three possible hybrid groups, as plausible morphological groups, though some are more distinct than others. While these groups have fairly geographically cohesive morphological patterns in which specimens can mostly be assigned easily based on geography, it is problematic to assign some specimens where these geographic areas come together. There is likely intergradation between some of these groups, which confounds classification and the ability to draw clear boundaries between them. Despite this, LDA had a relatively high percent of correct identifications for most groups and PERMANOVA found all groups to be significantly different based on the characters measured with the exception of those taxa with a very small sample size. One of the confounding issues with delineating taxa within *M. fasciculatus* sensu Bates is that most characters overlap between taxa and a combination of several characters is generally needed to distinguish them when taken out of a geographic context.

Despite exceptions to the rule and considerable overlap in many characters, general statements can be made for the character states of many morphological groups within *M. fasciculatus* sensu Bates. Some useful categorical characters from this study include inflorescence type, whether or not leaf lobing is obvious, leaf base shape, and how distinct the stellate trichome rays on the stem are without magnification (Table 6). Inflorescences can vary

from spike-like to panicle-like in the same group, however, some groups generally are one or the other. Leaves may vary from unlobed to obviously lobed within the same group, but a few groups tend towards more obvious lobing than others. Leaf bases may range from cordate to truncate to cuneate even on the same stem of a specimen, but some groups tend towards or away from certain leaf base shapes. Stellate trichome rays on the stem that are distinct without magnification set *M. arcuatus* and some "*fasciculatus*/*foliosus* intermediates" apart from the rest of *M. fasciculatus* sensu Bates, which have much shorter trichome rays. The density of stellate trichomes on the adaxial and abaxial leaf surfaces is also very useful to distinguish some groups in *M. fasciculatus* sensu Bates (Fig. 22). This can be confounded if sampled from leaves not fully expanded or sampled from the smaller and often denser-trichomed summer/fall leaves that emerge after the winter/spring leaves drop. However, in general, the trichome density of the adaxial and abaxial surfaces of fully expanded winter/spring leaves, as well as the relative trichome density between these surfaces, is very useful to distinguish some groups.

Table 6. Generalized categorical characters useful in distinguishing taxa within *M. fasciculatus* sensu Bates. See also the boxplot and barplot comparisons with all morphological groups in the "Utility of measured characters in distinguishing taxa" section of this paper (Chapter 4).

Morphological group	Inflorescence type	Leaf lobing	Leaf base	Stem stellate trichome ray distinctness without magnification
arcuatus	spike-like	Not to slightly lobed	Variable	Slightly to clearly distinct
hallii	spike-like to panicle-like	Generally slightly lobed	Variable	Generally not distinct
mendocinensis	spike-like to narrow panicle-like	Slightly to obviously lobed	Generally cordate	Not distinct
nuttallii	panicle-like	Generally obviously lobed	Variable	Not distinct
nesioticus	panicle-like	Generally obviously lobed	Generally cordate	Not distinct
laxiflorus	spike-like to panicle-like	Highly variable	Generally cordate	Not distinct
parishii	panicle-like	Slightly lobed	Cuneate	Not distinct
"Santa Rosa"	panicle-like	Slightly lobed	Cordate	Not distinct
catalinensis	spike-like to panicle-like	Generally obviously lobed	Generally cordate	Generally not distinct
fasciculatus s.s.	spike-like (sometimes with proximal spike-like branches)	Generally slightly lobed	Generally cordate	Generally not distinct
"Baja east"/fasciculatus intermediates	spike-like (sometimes with proximal spike-like branches)	Generally slightly lobed	Variable	Not distinct
fasciculatus/foliosus intermediates	spike-like to panicle-like	Generally slightly lobed	Variable	Variable

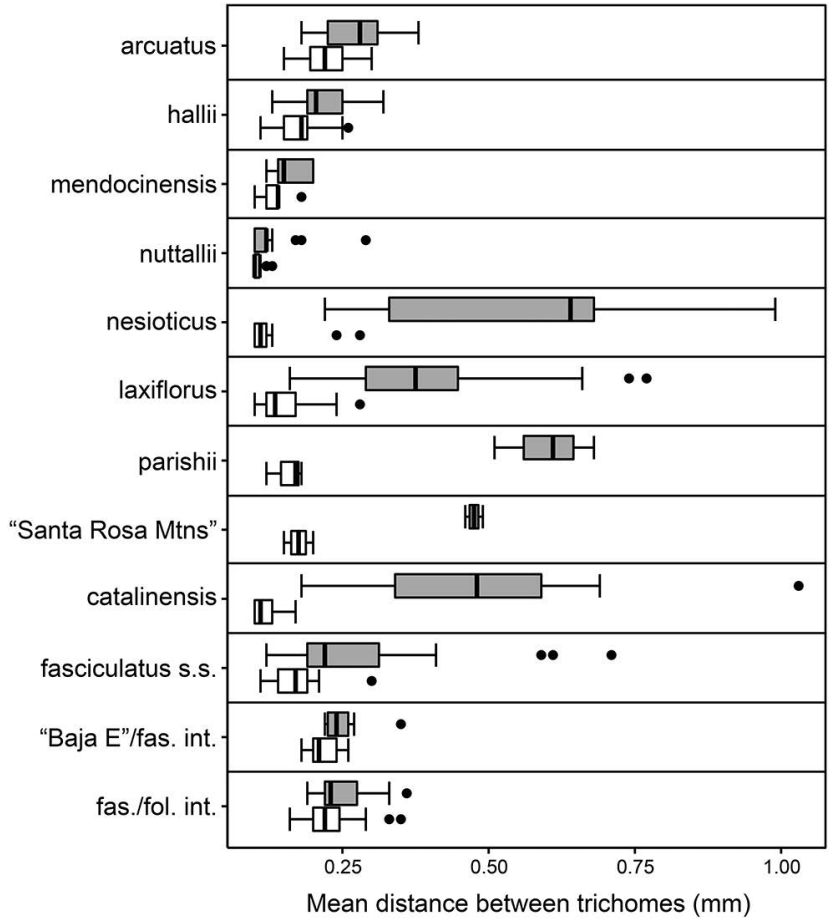

Figure 22. Mean distance in mm between centers of stellate trichomes on adaxial and abaxial leaf surfaces of morphological groups within *Malacothamnus fasciculatus* sensu Bates. Adaxial surface above with grey box and abaxial surface below with white box. Larger values indicate sparser trichomes. See also Figure 53 for boxplots showing the ratio of adaxial to abaxial leaf stellate trichome density for all morphological groupings.

3.3 *Malacothamnus davidsonii*

Malacothamnus davidsonii is distinguished from other *Malacothamnus* species by the combination of relatively short calyx bracts, relatively long stellate trichome rays, stout branches, relatively large plant size, and later blooming period (Kearney 1951; Bates 1963, 2015). *Malacothamnus davidsonii* is known from two regions in California disjunct by ~330 km. These two regions are analyzed with PCA, LDA, and PERMANOVA to assess morphological divergence between regions.

Populations in the southern region of *Malacothamnus davidsonii*, which includes the type locality, occur in Los Angeles County and populations in the northern region occur in Monterey and San Luis Obispo counties. While plants of these two regions appear to be the same species and may have been geographically connected at one point, the current disjunction prevents geneflow between these regions. Assuming *M. davidsonii* plants from both of these regions have the same origin, hybridization with other species in these regions after separation may have contributed to divergence. In the southern region, *M. davidsonii* occurs

with *M. fasciculatus* var. *laxiflorus*. While *M. davidsonii* generally flowers later than *M. fasciculatus* var. *laxiflorus*, their flowering times occasionally overlap and morphologically intermediate plants can be found, especially where they are sympatric. In the northern region, *M. davidsonii* can be found with both *M. jonesii* and *M. abbottii*. While *M. jonesii* is done flowering well before *M. davidsonii* starts, the flowering times of *M. davidsonii* and *M. abbottii* overlap considerably, though there are no clearly morphologically intermediate plants between these two species known.

PCA of *Malacothamnus davidsonii* shows plants from the two regions mostly divided along the PC1 axis with some overlap (Fig. 23). The northern specimens form a relatively tight cluster, while the southern specimens are much more spread out in the plot. The lectotype plots within the PC1 overlap area between northern and southern specimens. PC1 explains 17.8% of the variation with the highest-weighted characters being stellate trichome ray length on the calyx and stem, glandular trichome length on the stem, and calyx width (Appendix 2).

LDA comparing the two regions of *Malacothamnus davidsonii* shows six specimens from each region misclassified (Table 7). PERMANOVA indicates differences between the two regions are significant (SumsOfSqs = 0.2, pseudo-F = 6.4, R^2 = 0.13, *p*-value = 0.001).

Evidence from PCA and PERMANOVA shows that the disjunct northern and southern populations of *Malacothamnus davidsonii* are significantly different morphologically. However, some overlap in the PCA and misidentifications of 28% of specimens in the LDA indicate that confidently differentiating these groups based on the characters measured could prove problematic. Morphological clustering by region seen in the PCA indicates the possibility of morphological divergence within one taxon or morphological convergence between two taxa. Whether it is appropriate to recognize plants from these two regions as different taxa needs to be further assessed with molecular analyses. Examination of characters measured finds glandular trichome length on the calyx and calyx lobe size can help distinguish plants from these two regions, but not consistently. The only clear distinction appears to be geographic, which could be confounded if plants from one region are introduced into another region.

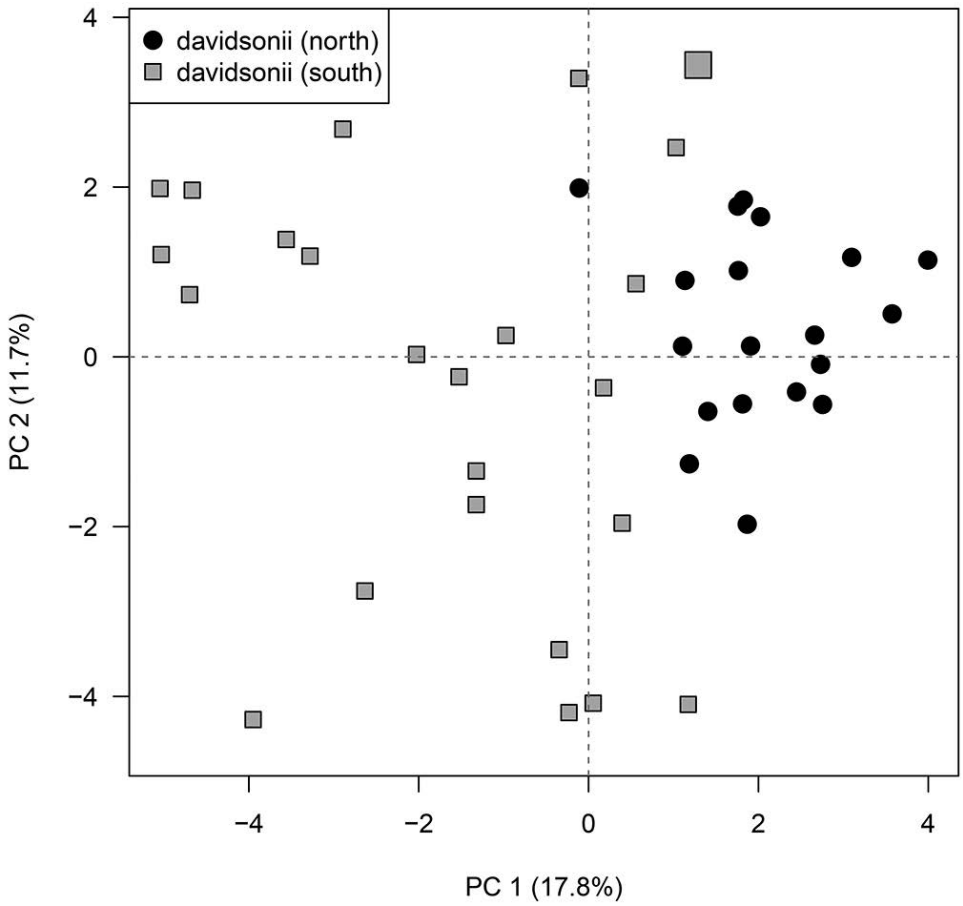

Figure 23. PCA results comparing morphology of the northern and southern regions of *Malacothamnus davidsonii*. The larger square denotes the lectotype.

Table 7. Predicted vs. actual group results of LDA comparing specimens from the northern and southern *Malacothamnus davidsonii* regions. Blue with bold numbers indicates a correct prediction and yellow indicates an incorrect prediction.

	Predicted group			
Actual groups	davidsonii N	davidsonii S	Total	Percent correctly identified
davidsonii N	**13**	6	19	68%
davidsonii S	6	**18**	24	75%

3.4 *Malacothamnus densiflorus* sensu Bates

Malacothamnus densiflorus sensu Bates is distinguished from all other *Malacothamnus* species by the combination of long and few-rayed stellate trichomes on the calyx, relatively sparse stellate trichomes, and an interrupted-spicate inflorescence (Bates 1963, 2015). *Malacothamnus densiflorus* sensu Bates is assessed using PCA, LDA, and PERMANOVA to clarify finer-scale morphological groupings within the species.

Two basionyms are included under *Malacothamnus densiflorus* sensu Bates, which were treated as *M. d.* var. *densiflorus* and *M. d.* var. *viscidus* by Kearney (Fig. 1). Distinguishing *M. d.* var. *viscidus* from the rest of the species has long been a point of confusion. Kearney (1951), despite recognizing *M. d.* var. *viscidus*, notes "intergradation with typical *M. densiflorus* is complete, however, and specimens of more or less intermediate character are about as numerous as specimens of the typical phase and of var. *viscidus*". Bates (1963) notes extensive intergradation of *M. densiflorus with M. fasciculatus* s.s. where they occur in close proximity, which may further confuse matters. Examination of specimens of *M. densiflorus* sensu Bates showed plants from near the type locality of *M. d.* var. *viscidus* to have a generally different appearance from the rest of the species with relatively long glandular trichomes standing out as a possible distinctive character. I used plants with long glandular trichomes from this region as my hypothesized grouping assigned to *M. d.* var. *viscidus*.

PCA was run on all *Malacothamnus densiflorus* sensu Bates specimens including three specimens classified as *M. densiflorus* by Morse and Chester (2019) that appear somewhat intermediate with *M. fasciculatus* s.s. (Fig. 24). This PCA shows strong separation of *M. d.* var. *viscidus* from the rest on PC1 except for one specimen identified as *M. d.* var. *viscidus* plotting intermediately, which could possibly be a hybrid with *M. d.* var. *densiflorus* or *M. fasciculatus* s.s. but most closely fits *M. d.* var. *viscidus* on visual inspection. PC1 explains 23.9% of the variation with the highest-weighted characters being the length of glandular trichomes on the calyx, the density of stellate trichomes on the calyx tube, and the length of stellate trichome rays on the stem (Appendix 2). PC2 explains 15.1% of the variation with the highest-weighted characters being the length of the calyx and bracts as well as the length of stellate trichome rays on the calyx. Interestingly, the couplet Kearney (1951) used to distinguish the *M. densiflorus* varieties included calyx length with *M. d.* var. *densiflorus* being 10–14 mm and *M. d.* var. *viscidus* being 7–10 mm. My measurements show calyx lengths of 8–14.5 mm for *M. d.* var. *densiflorus* and 8–16.5 mm for *M. d.* var. *viscidus* showing this division to be a point of confusion between the varieties. The delineation of these varieties using Kearney's key appears to be mostly between more and less robust plants in the species or extremes on a spectrum, rather than between the varieties themselves, and roughly corresponds with PC2. This clearly highlights the need for recircumscription of the varieties using the high-weighted characters of PC1. Three geographic regions of *M. d.* var. *densiflorus* are further explored without *M. d.* var. *viscidus*.

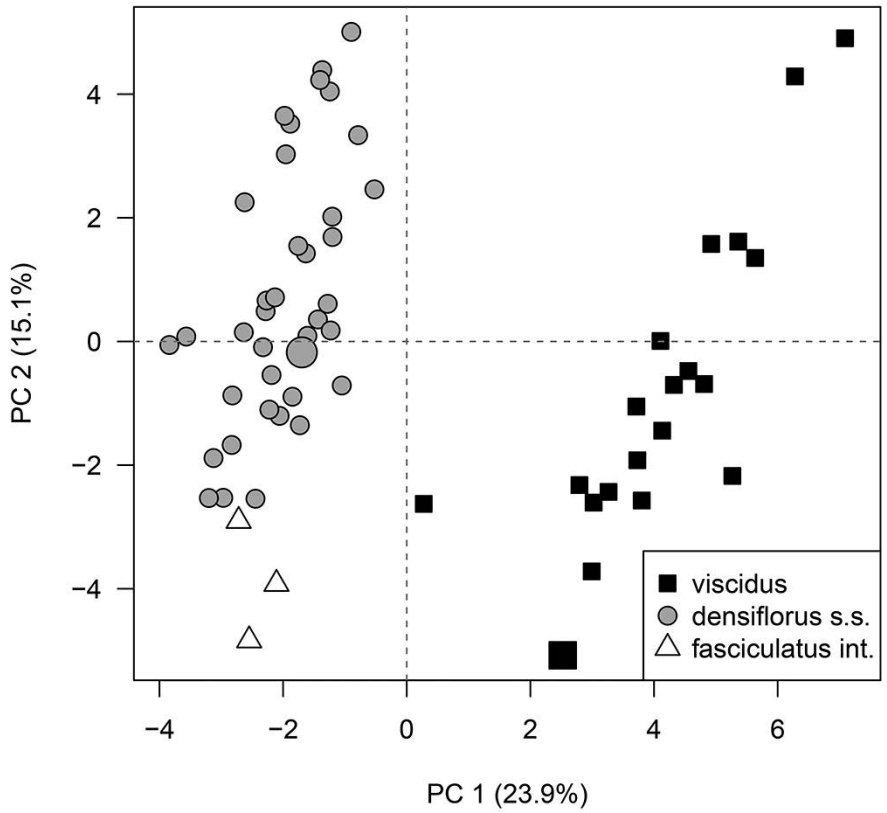

Figure 24. PCA results comparing morphology of *Malacothamnus densiflorus* var. *viscidus* to the remainder of *Malacothamnus densiflorus* sensu Bates and possible intermediates with *M. fasciculatus* s.s. Larger symbols denote type specimens.

The lectotype of *Malacothamnus densiflorus* is from the San Jacinto Mountains in Riverside County, CA. This location is somewhat disjunct (~35 km) from the rest of *Malacothamnus densiflorus* sensu Bates and divided from it by a region where only *M. fasciculatus* var. *laxiflorus* is known to occur. Before a recent discovery of a population of *M. densiflorus* in the San Jacinto Mountains after a burn, only three collections had been made there, these in 1882 and 1901. This newly found population looks somewhat different from the rest of the live plants I have seen of *M. d.* var. *densiflorus*, particularly in trichome color, which was not measured for this study. I've included several specimens from this population to assess whether the lectotype fits better with these specimens than the rest of the genus and whether plants from the San Jacinto Mountains are distinct from the rest of *M. d.* var. *densiflorus*. The remainder of *M. d.* var. *densiflorus* can be separated into two geographic areas: plants from San Diego County including adjacent Baja California to the south and the northern edge of Palomar Mountain to the north (referred to below as the San Diego County region) and plants from and adjacent to the Santa Ana Mountains in Orange and Riverside counties, CA (referred to below as the Santa Ana Mountain region). Measured specimens are mapped by morphological and geographic groups in Fig. 25.

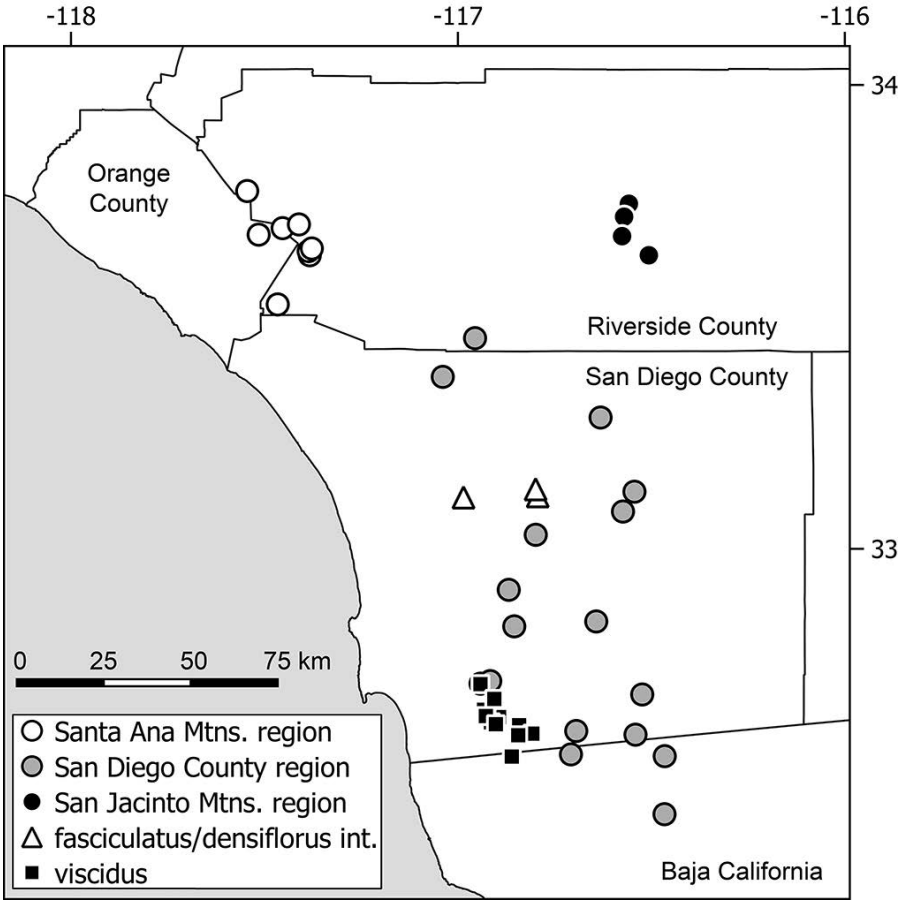

Figure 25. Map of specimens measured in *Malacothamnus densiflorus* sensu Bates broken into morphological and geographic groups. Circles represent the three regions of *M. d.* var. *densiflorus* with the San Jacinto Mountains being the type locality. Also included are possible intermediates with *M. fasciculatus* s.s.

PCA of all *Malacothamnus densiflorus* sensu Bates excluding *M. d.* var. *viscidus* shows some separation of specimens from the San Jacinto Mountains region from the other geographic regions as well as some separation of the possible *M. fasciculatus* s.s. intermediates (Fig. 26). Specimens apparently intermediate with *M. fasciculatus* s.s. plot on one extreme of the PC1 axis and are characterized by shorter stellate trichome rays and glandular trichomes on the calyx, denser stellate trichomes on the calyx tube, and shorter calyces and stipular bracts (Appendix 2). All of these characters indicate likely intermediacy with *M. fasciculatus* s.s. The PC2 axis mostly separates plants from the San Jacinto Mountains region from the other regions. Despite generally higher PC2 values, the Santa Ana Mountains region plots within the variation of the San Diego County region. Highly weighted characters on the PC2 axis include stellate trichome ray and glandular trichome lengths on both the stem and calyx, longest inflorescence internode, and longest inflorescence branch. No further separation of geographic groups is seen on other PC axes. A further PCA without the *M. fasciculatus* s.s. intermediates (Fig. 27) shows the same separation between the *M. d.* var. *densiflorus* regions but on the PC1 axis and with the separation of the San Jacinto Mountains region from the rest somewhat greater.

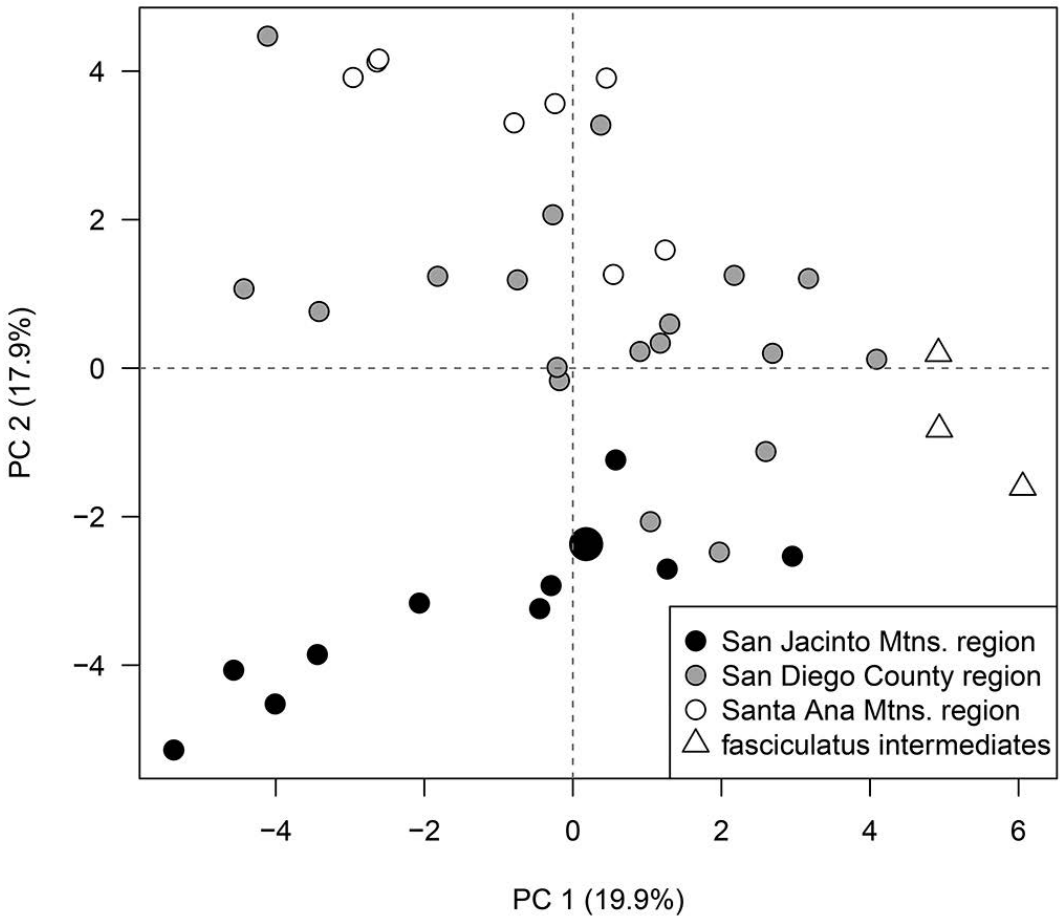

Figure 26. PCA results comparing morphology of three regions of *Malacothamnus densiflorus* sensu Bates excluding *M. densiflorus var. viscidus* and including three specimens possibly intermediate with *M. fasciculatus* s.s. The larger circle denotes the lectotype of *M. densiflorus*.

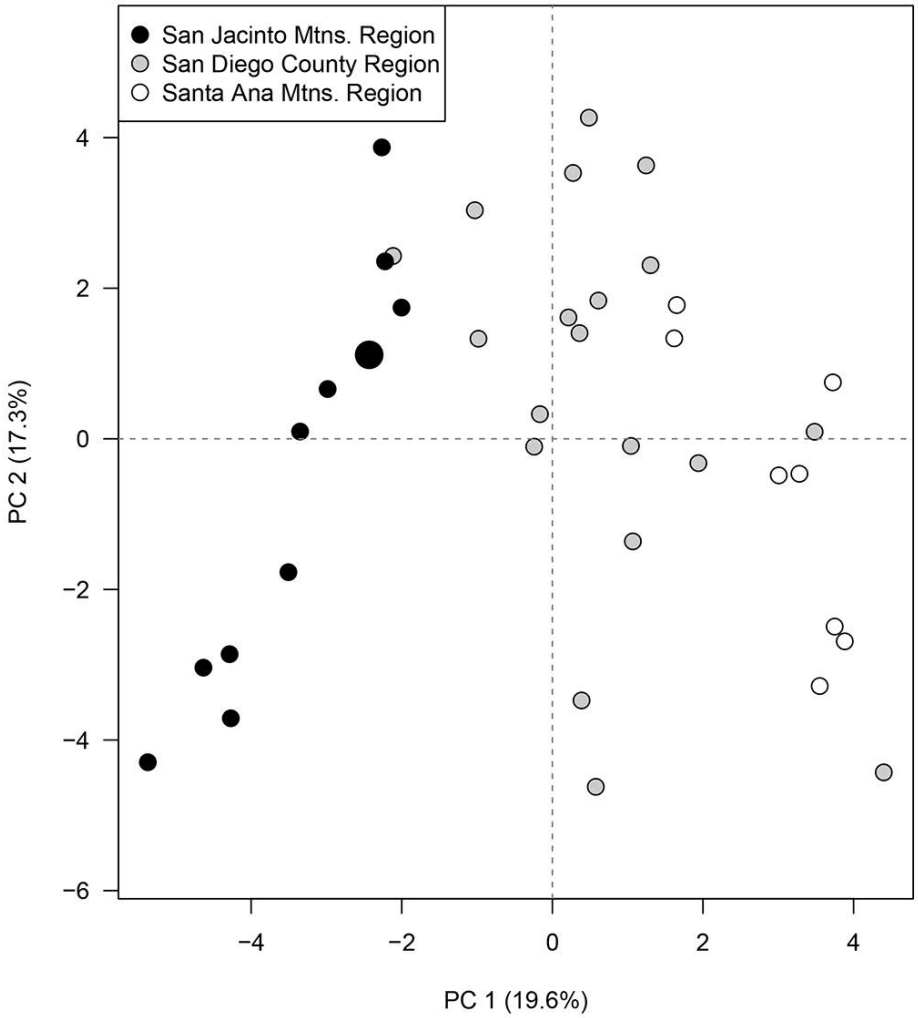

Figure 27. PCA results comparing morphology of three regions of *Malacothamnus densiflorus* sensu Bates excluding *M. densiflorus var. viscidus* and three specimens possibly intermediate with *M. fasciculatus* s.s. The larger circle denotes the lectotype of *M. densiflorus*.

LDA was run using all specimens of *Malacothamnus densiflorus* var. *viscidus* (including the possible hybrid) and the three regional groups of *M. d.* var. *densiflorus* used in the PCAs (Table 8). The possible intermediates between *M. d.* var. *densiflorus* and *M. fasciculatus* s.s. were excluded. All specimens of *Malacothamnus densiflorus* var. *viscidus* were predicted correctly by the LDA. At least one specimen within all regional groups of *M. d.* var. *densiflorus* was predicted incorrectly. All were predicted correctly at least 73% of the time.

PERMANOVA was run using the same set of specimens and groupings as the LDA (Table 9). All pairwise comparisons were significant. The pseudo *F*-ratio indicates *Malacothamnus densiflorus* var. *viscidus* was the most distinct in all comparisons and the San Diego region vs. Santa Ana Mtns. region was the least distinct.

Table 8. Predicted vs. actual group results for LDA of *Malacothamnus densiflorus* sensu Bates. Blue with bold numbers indicates a correct prediction and yellow indicates an incorrect prediction.

	Predicted group					
Actual group	Santa Ana Mtns. Region	San Diego County Region	San Jacinto Mtns. Region	viscidus	Total	Percent correctly identified
Santa Ana Mtns. Region	**7**	1	0	0	8	88%
San Diego County Region	2	**14**	3	0	19	74%
San Jacinto Mtns. Region	1	2	**8**	0	11	73%
viscidus	0	0	0	**20**	20	100%

Table 9. PERMANOVA results from pairwise comparisons of morphological groups in *Malacothamnus densiflorus* sensu Bates ordered by pseudo *F*-ratio.

pairs	SumsOfSqs	pseudo-*F*	R*2*	*p*-value
San Diego County Region vs viscidus	0.81	28.4	0.43	0.001
Santa Ana Mtns. Region vs viscidus	0.71	23.8	0.48	0.001
San Jacinto Mtns. Region vs viscidus	0.62	23.0	0.44	0.001
Santa Ana Mtns. Region vs San Jacinto Mtns. Region	0.38	10.9	0.39	0.001
San Diego County Region vs San Jacinto Mtns. Region	0.23	5.9	0.17	0.001
San Diego County Region vs Santa Ana Mtns. Region	0.14	3.6	0.13	0.002

Evidence from PCAs, LDA, and PERMANOVA of *Malacothamnus densiflorus* sensu Bates indicates *M. d.* var. *viscidus* is clearly morphologically distinct from the rest of the species with a mostly distinct range immediately adjacent to and slightly overlapping with other plants within the species. Plants of *M. d.* var. *viscidus* as well as plants of *M. d.* var. *densiflorus* from both the San Jacinto Mountains and San Diego County were grown from seed at California Botanic Garden to test whether environmental variables from their collection sites induced their distinctive morphologies. All three groups retained the morphology from their home range in the garden plantings.

Confusion between the varieties of *Malacothamnus densiflorus* likely stems at least partly from the protolog of *Malvastrum viscidum* (currently *M. d.* var. *viscidus*) where, after describing *Malvastrum viscidum* from El Nido (near Otay Mountain in San Diego County), the author notes that a Nevin specimen (GH00420507) from San Juan Capistrano in Orange County, CA also belongs in *Malvastrum viscidum* (Abrams 1907). Plants from the Otay Mountain region have much longer glandular trichomes than the rest of *Malacothamnus densiflorus* as well as

much-denser stellate trichomes on the calyx tube, the combination of which may readily distinguish these from the rest of the species. Examination of a high-resolution scan of the Orange County specimen referred to by Abrams in the *Malvastrum viscidum* protolog shows it to have sparse stellate trichomes on the calyx tube and no apparent long glandular trichomes, which fits with *M. d.* var. *densiflorus* and not *M. d.* var. *viscidus*.

The remaining regional groupings in *Malacothamnus densiflorus* all show some patterns of morphological variation that could possibly be attributed to divergence but whether that level of divergence is worthy of recognition at a taxonomic rank or whether it may just be variation between populations needs to be assessed further with molecular methods. Plants from the San Jacinto Mountains appear to be most distinct from the rest. Plants from the San Diego and Santa Ana Mountain regions seem to be the most cohesive. Boxplots of all characters examined between the three regions show patterns for many characters but with overlap in all characters. Individually, the most distinct characters assessed distinguishing the San Jacinto Mountains plants from plants of the other two regions are the longest inflorescence branch length and the mean stellate trichome ray length on the stems, both characters generally being longer in the San Jacinto plants. Plants from the Santa Ana Mountains region generally have sparser stellate trichomes on the leaves than the other two regions. I carry forward the San Jacinto Mountains plants as a separate group for further analysis with the full genus as this group includes the type specimen and they are mostly distinct in the PCAs, though the type is similar to some San Diego specimens in the PCAs. I combine the Santa Ana Mountains and San Diego groups in further analyses based on high overlap in the PCAs.

As previous treatments confused the distinctions between *Malacothamnus densiflorus* var. *viscidus* and the rest of *M. densiflorus*, I provide here new diagnostic characters to distinguish the varieties using dry measurements. *Malacothamnus densiflorus* var. *viscidus* has many glandular trichomes on the stem and calyx ≥ 0.3 mm, and generally dense stellate trichomes on the calyx tube. *Malacothamnus densiflorus* var. *densiflorus* has all glandular trichomes on the stem ≤ 0.1 mm, all glandular trichomes on the calyx ≤ 0.4 mm, and generally sparse stellate trichomes on the calyx tube. More detailed comparisons of characters between the varieties are shown with the full genus later in this paper.

3.5 *Malacothamnus marrubioides* and *M. foliosus* sensu Bates

Malacothamnus marrubioides is distinguished from all other *Malacothamnus* species by the combination of relatively long calyx bracts, relatively long and narrow calyx lobes, short and dense stellate trichomes, and a spike-like inflorescence (Bates 1963, 2015). *Malacothamnus marrubioides* generally includes the basionym *Malvastrum gabrielense*, which has not been treated as a distinct taxon since the 1930s (Eastwood 1936). *Malacothamnus foliosus* sensu Bates (including *M. paniculatus*) is distinguished from the rest of the genus by the combination of relatively wide calyx lobes that give the flower buds an angled to winged appearance, the calyx lobes being abruptly pointed at the tip, and the calyx bracts being linear (Bates 1963). Morphological extremes of *Malacothamnus foliosus* with narrower calyx lobes closely resemble *M. marrubioides,* which has led to *M. foliosus* sensu Bates being included in *M. marrubioides* in the past (Gray 1886). Both *M. marrubioides* and *M. foliosus* sensu Bates are assessed using PCA,

LDA, and PERMANOVA to clarify how distinct they are from each other and to clarify finer-scale morphological groupings within *M. foliosus* sensu Bates.

The type locality of *Malacothamnus marrubioides* is purported to be from Fort Miller in Fresno County, CA (Durand and Hilgard 1855). This location, known only from a single collection from July 1854, is disjunct by over 300 km from all other confirmed locations of *M. marrubioides*, which occur in Los Angeles and Ventura counties, primarily in the watershed feeding into the Santa Clara River. The expedition in which the type specimen was collected also passed through the Santa Clara River watershed in September 1854, which could be the true origin of the type collection (Williamson et al. 1856). September would be late in the season for a blooming plant, but *Malacothamnus* populations often have a few stems that flower outside the peak blooming season. If the type specimen was collected from outside the Santa Clara River watershed, morphological analyses may show it to be distinct from the rest. If the morphology of the type specimen fits within the variation of the rest, this may provide evidence of the possibility, but not necessarily indicate, that an erroneous type locality was recorded in the protologue.

The type of *Malvastrum gabrielense* was collected from Arraster, CA in the Santa Clara River watershed and has been generally recognized as a synonym of *Malacothamnus marrubioides*. *Malacothamnus marrubioides* (then *Malvastrum*) is not mentioned in the protolog of *Malvastrum gabrielense* and the authors note *Malvastrum gabrielense* appears to lack obvious relationships with other taxa (Munz and Johnston 1925). This implies the authors were possibly unaware of *M. marrubioides*.

To assess whether the morphology of the types of either *Malacothamnus marrubioides* or *Malvastrum gabrielense* fell outside of the variation of a broader sampling of *M. marrubioides*, PCA was performed on 21 specimens of what is currently considered *M. marrubioides* including an isotype of *M. marrubioides* and two type specimens (holo- and iso-) of *Malvastrum gabrielense* (Fig. 28). No clear clustering was evident and the types of both *M. marrubioides* and *Malvastrum gabrielense* fell within the variation of the rest of the sampled specimens on the first six PC axes. This supports a hypothesis of *M. marrubioides* and *Malvastrum gabrielense* belonging to a single morphological group and provides evidence that the disjunct locality of the *M. marrubioides* type collection may be incorrect or that *M. marrubioides* has (or had) a wider range than has been documented in all collections since the type collection.

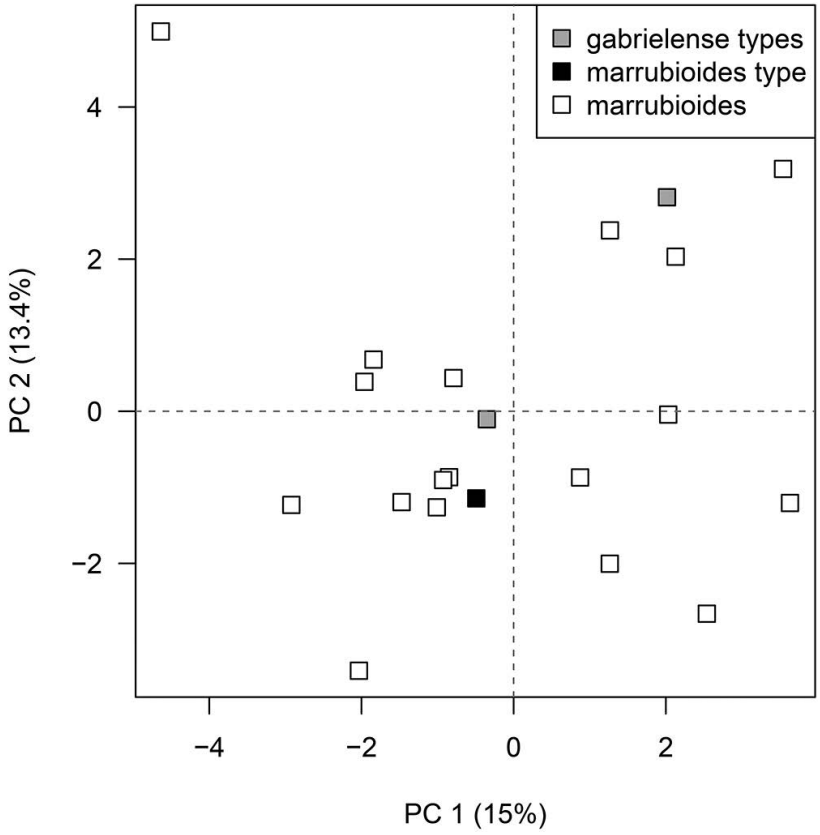

Figure 28. PCA results comparing morphology of nontype specimens of *Malacothamnus marrubioides* with types of *M. marrubioides* and *Malvastrum gabrielense*.

Both species within *M. foliosus* sensu Bates (*M. foliosus* s.s. and *M. paniculatus*) have been included in *M. marrubioides* in the past. The basionym of *M. paniculatus* was originally described as a variety of *M. marrubioides* (then *Malvastrum*) and *M. foliosus* was relegated to a synonym of *M. marrubioides* in the same paper (Gray 1886). However, Wiggins (1950) argued that both deserved to be treated at the species rank saying that *M. paniculatus* "bears only a superficial resemblance to *M. marrubioides*" and of *M. foliosus* that "certainly it is not conspecific with *M. marrubioides*". Kearney (1951) followed Wiggins treating *M. foliosus* and *M. paniculatus* as separate species. Bates (1963) suggested and Fryxell (1988) treated *M. foliosus* and *M. paniculatus* as the single species *M. foliosus* with no subtaxa. Slotta (2004) recognized *M. paniculatus* but included *M. foliosus* in *M. fremontii* without explanation. Contrarily, Slotta annotated the *M. foliosus* lectotype (GH00052896) as *M. paniculatus* and a *M. foliosus* isolectotype (UC109091) as *M. marrubioides*. Based on this taxonomic history, *M. foliosus* sensu Bates is assessed with *M. marrubioides* to clarify if these two species are morphologically distinct.

PCA of *M. foliosus* sensu Bates and *M. marrubioides* shows each group is clearly separated along PC1 (Fig. 29). While *M. foliosus* sensu Bates is spread out along PC2 indicating

possibly more than one morphological group, *M. marrubioides* forms a relatively tight cluster. PC1 explains 30.3% of the variation with a wide variety of highly weighted characters including inflorescence branch length, calyx lobe width, calyx bract length, stellate trichome ray length on calyx, glandular trichome length on calyx, and calyx lobe trichome density (Appendix 2). PC2 explains 12.6% of the variation with the highest-weighted characters being calyx and calyx lobe length. Note that the four stems measured from two *M. foliosus* type specimens are the most likely of any *M. foliosus* sensu Bates specimens to be confused with *M. marrubioides* and they separate from *M. marrubioides* on both the PC1 and PC2 axes.

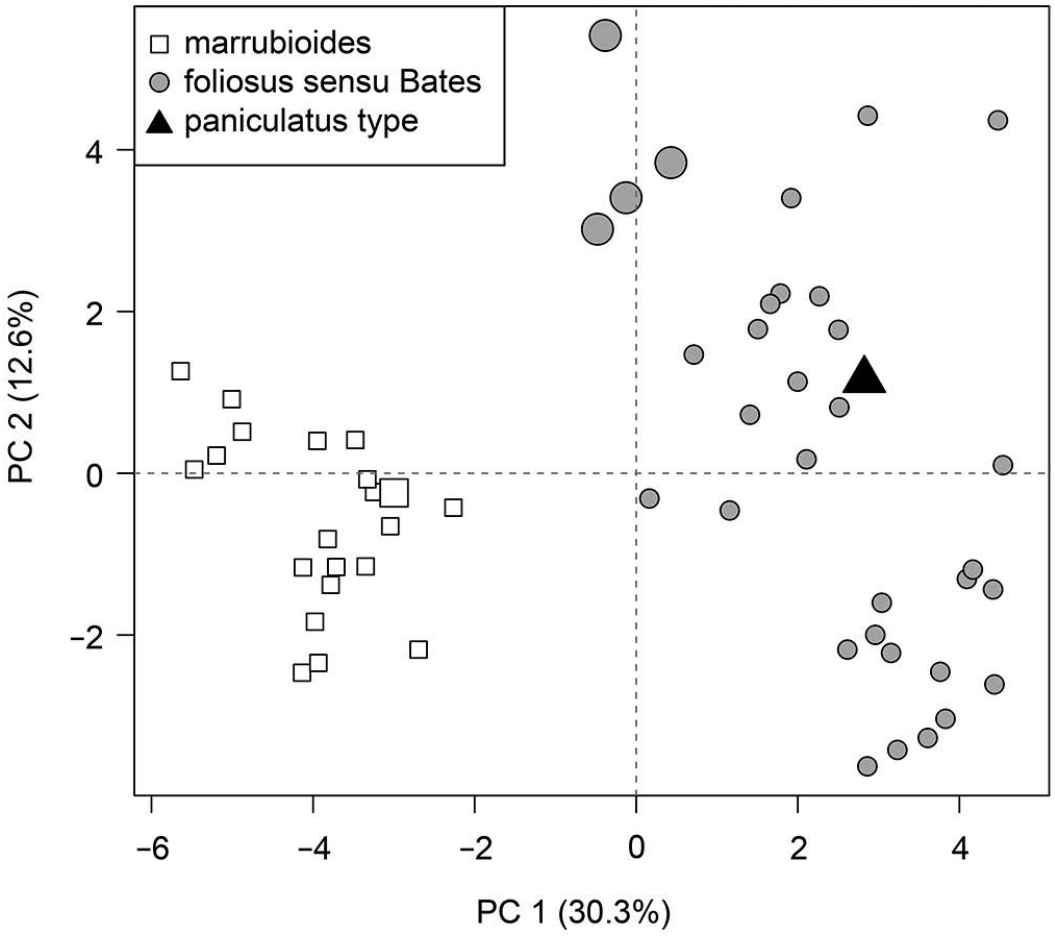

Figure 29. PCA results comparing morphology of *Malacothamnus marrubioides* with *M. foliosus* sensu Bates. Larger symbols denote type specimens.

Malacothamnus foliosus sensu Bates can be roughly divided into three morphological and geographic groups: a coastal group, an inland group excluding the type locality, and the *M. foliosus* type locality. Plants growing closer to the coast with paniculate inflorescences and wider calyx lobes have been attributed to *M. paniculatus*. The *M. foliosus* type locality is inland and somewhat disjunct to the south of all others. These form the other morphological extreme with spike-like inflorescences and narrower calyx lobes. The remaining inland specimens form an east/west distribution with the coastal specimens and appear somewhat morphologically intermediate between the coastal specimens and the *M. foliosus* type specimens. The PC1 axis on a PCA of *M. foliosus* sensu Bates mostly supports these groupings (Fig. 30). Plotting PC1 values versus longitude shows the more-coastal specimens to have higher PC1 values and the more-inland specimens to have lower PC1 values with the somewhat disjunct *M. foliosus* type specimens having the lowest PC1 values (Fig. 31).

Two specimens do not follow this pattern. One is a morphological outlier and the longitude of the other may be incorrect. SD109026 is a more coastal specimen that plots with the more inland specimens on PC1. This specimen generally fits with the other more coastal specimens but is an extreme outlier in some measurements for both groups. While the location of the *M. paniculatus* type is also plotted as more coastal, the collector's location description is vague. This type specimen's true origin was likely more inland, which is possibly supported by another *M. foliosus* sensu Bates specimen (BM000939051) fitting the morphology of more eastern plants that was collected the previous day by the same collector. A gap in the PC1 values between more coastal and inland plants also corresponds with a small geographic gap. If this is a true geographic gap, the gap along PC1 may indicate a real morphological gap but, if additional plants were found in this geographic gap, perhaps these plants would also be intermediate in PC1 values.

One collection of inland *M. foliosus* has four specimens measured with PC2 values ranging from 3.6 to -2.1. Assuming other populations have this much variation on PC2, all plants with a negative PC1 value could arguably be classified as a single group with the *M. foliosus* types being the most extreme on PC1 and the *M. paniculatus* type showing one of two extremes on PC2. This would yield two groups, an inland *M. foliosus* that includes all type specimens of both species, and a coastal *M. foliosus* that does not include any type specimens. Almost perfect separation between these coastal and inland groups can be seen by plotting the length of the longest stellate trichome rays on the calyx against the ratio of the calyx lobe length to width (Fig. 32). For further analyses, I use a coastal *M. foliosus* group including the coastal specimen (SD109026) that is an outlier on the PC1 axis and an inland *M. foliosus* group including the types of both *M. foliosus* and *M. paniculatus*.

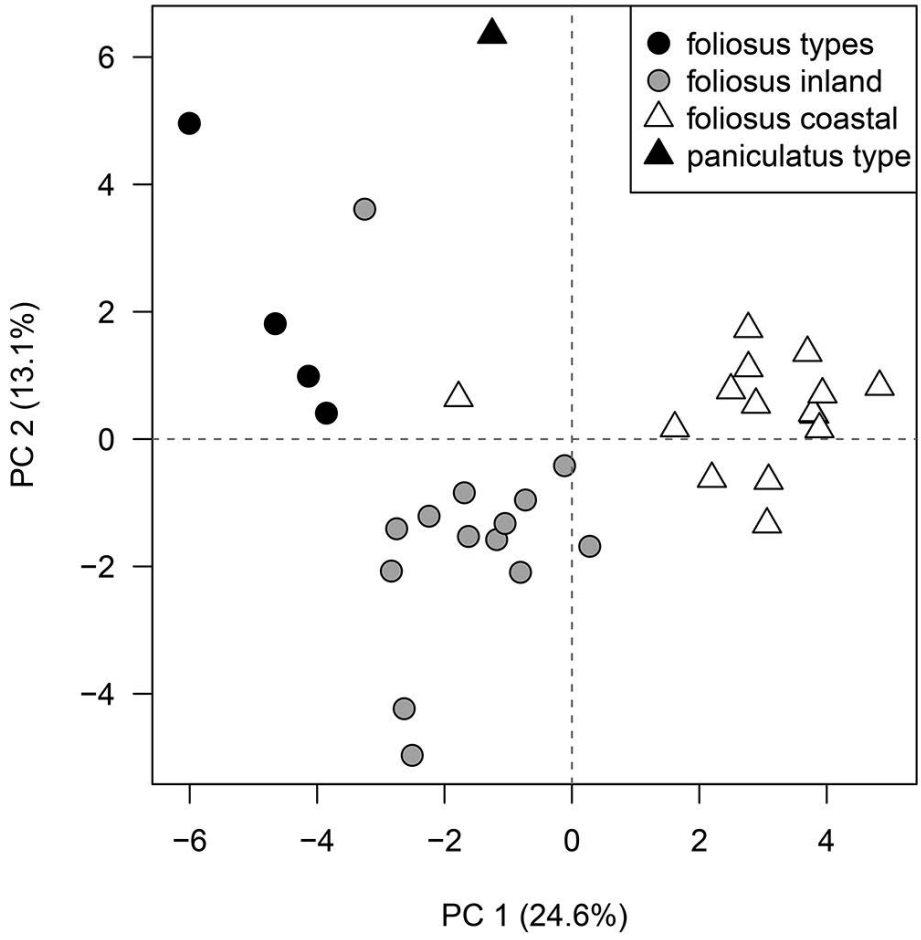

Figure 30. PCA results comparing morphology of specimens within *M. foliosus* sensu Bates.

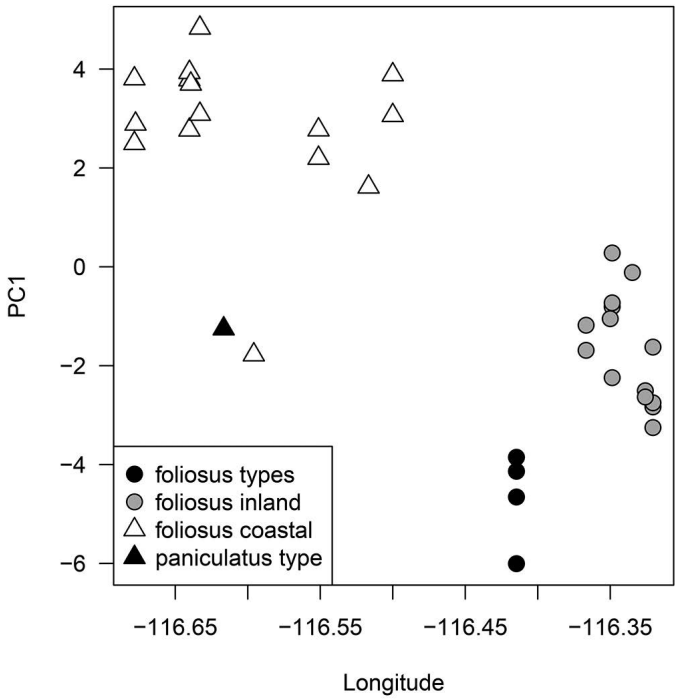

Figure 31. PC1 values from Figure 30 plotted against longitude shows a general pattern in PC1 values by location except for the *Malacothamnus paniculatus* type and one coastal *M. foliosus* outlier. Note that the *M. paniculatus* type location is vague, so possibly could have been collected from a more eastern location.

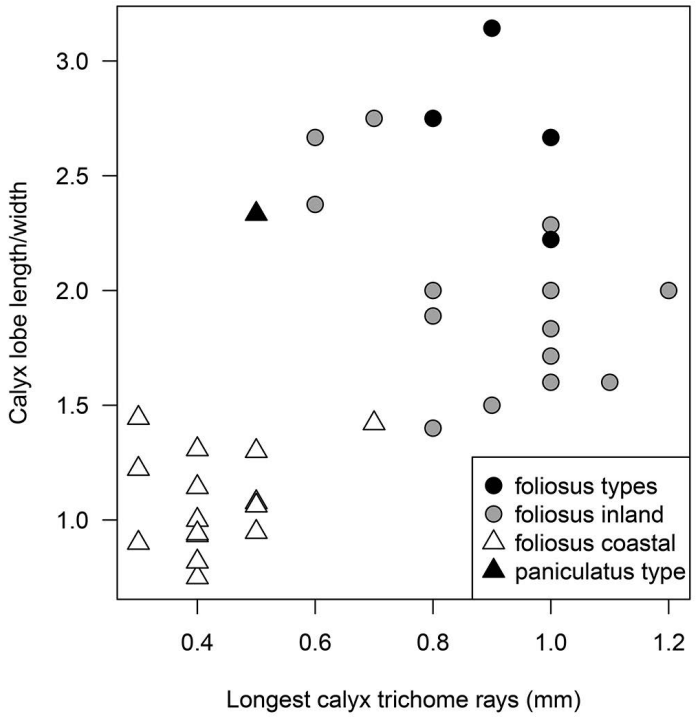

Figure 32. Scatterplot of *Malacothamnus foliosus* sensu Bates plotting length of the longest stellate trichome rays on the calyx against the ratio of the calyx lobe length to width. The combination of these two characters almost perfectly separates the more coastal *M. foliosus* from the rest.

LDA was run including all specimens of *M. marrubioides* and *M. foliosus* sensu Bates. *Malacothamnus foliosus* sensu Bates was divided into a coastal group without any type specimens and an inland group including the types for both *M. foliosus* and *M. paniculatus* (Table 10). LDA resulted in only one misclassification based on these groups. As in Fig. 30, the outlier specimen SD109026 was assigned to the inland *M. foliosus* group rather than the coastal group it was classified as.

PERMANOVA was run using the same set of specimens and groupings as the LDA (Table 11). All pairwise comparisons were significant with the two *M. foliosus* groupings being most similar based on the pseudo *F*-ratio.

Table 10. Predicted vs. actual group results of LDA comparing specimens from *Malacothamnus foliosus* sensu Bates and *M. marrubioides*. Blue with bold numbers indicates a correct prediction and yellow indicates an incorrect prediction.

	Predicted group				
Actual group	foliosus coastal	foliosus inland	marrubioides	Total	Percent correctly identified
foliosus coastal	**14**	1	0	15	93%
foliosus inland	0	**19**	0	19	100%
marrubioides	0	0	**21**	21	100%

Table 11. PERMANOVA results from pairwise comparisons of morphological groups in *Malacothamnus foliosus* sensu Bates and *M. marrubioides* ordered by pseudo *F*-ratio.

pairs	SumsOfSqs	pseudo-*F*	R2	*p*-value
foliosus coastal vs marrubioides	1.04	55.8	0.62	0.001
foliosus inland vs marrubioides	0.61	25.4	0.40	0.001
foliosus coastal vs foliosus inland	0.38	11.9	0.27	0.001

Evidence from PCA indicates that *Malvastrum gabrielense* has been correctly treated as a synonym of *M. marrubioides*. Evidence from PCAs, LDA, and PERMANOVA indicates that *M. marrubioides* is distinct from *M. foliosus* sensu Bates and that *M. foliosus* sensu Bates is perhaps reasonably treated as two morphological groups, one more coastal with no type specimens and one more inland including the types of both *M. foliosus* and *M. paniculatus*. The type of *M. paniculatus*, however, is an outlier, is possibly intermediate, and could arguably be assigned to either group. Based on the PCA and its various outliers, *M. foliosus* sensu Bates could also represent a single highly variable group or possibly even three groups represented by the coastal plants, the *M. foliosus* types, and a third group somewhat intermediate between them that may include the *M. paniculatus* type. This will have to be clarified with DNA analyses, though this is complicated by the fact that no recent specimens clearly fit the morphology of

either the *M. foliosus* or *M. paniculatus* type specimens and no specimens have been collected from the type locality of *M. foliosus* after the original collection. For the present, the coastal and inland groupings as outlined in the analyses are a reasonable hypothesis of two different taxa or morphologically distinct populations that likely intergrade.

3.6 *Malacothamnus fremontii* sensu Bates

Malacothamnus fremontii sensu Bates is the most poorly defined of Bates's species. This species is distinguished from all other *Malacothamnus* species based on the combination of narrow calyx bracts, relatively long and narrow calyx lobes, calyces that are not angled or winged in bud, relatively long and sparse stellate trichomes, a relatively high number of stellate trichome rays on the calyx, and by having greater than six flowers clustered at each inflorescence node (Bates 1963, 2015). *Malacothamnus fremontii* sensu Bates is assessed using PCA, LDA, and PERMANOVA to clarify finer-scale morphological groupings within the species.

Bates (2015) treated seven basionyms in synonymy with *Malacothamnus fremontii* with no infraspecific taxa (Fig. 1). Kearney (1951) treated this same group as four species: *M. fremontii*, *M. helleri*, *M, howellii*, and *M. orbiculatus*. Slotta (2004, 2012), recognizing only two taxa, split *M. orbiculatus* back out from Bates' inclusion in *M. fremontii*, but her annotations of the two species are not geographically consistent with Kearney's treatment of the same species. Highly disjunct specimens from northwestern and central Arizona, erroneously called *M. fasciculatus* when the discovery was published (Hunkins and Smith 2012), most closely resemble *M. orbiculatus* and are here assessed as such. The basionym *Sphaeralcea fremontii* var. *exfibulosa* is presumably the same as *M. helleri*, which was published just five months earlier. Kearney (1951) treated *Malacothamnus howellii* with no infraspecific taxa and included both *Malvastrum fremontii* subsp. *cercophorum* and *Malvastrum howellii* var. *cordatum* as synonyms. Additionally, two possible undescribed species are included in *M. fremontii* sensu Bates. While Slotta (2004) doesn't discuss it, her identification of a specimen from Shasta County, CA is listed as "unknown", and examination of specimens treated as *M. fremontii* from this area suggest a morphologically distinct group. Likewise, specimens from Vandenberg Space Force Base (Vandenberg) in Santa Barbara County, CA treated within *M. fremontii* appear distinct and have been suggested as a possible new species in the past (Smith 1976; Howald et al. 1985).

PCA was run on all specimens measured of *M. fremontii* sensu Bates with groupings following Kearney plus the addition of the unnamed Vandenberg and Shasta County groups, type specimens of *Sphaeralcea fremontii* var. *exfibulosa* and *Malvastrum howellii* var. *cordatum*, and two specimens that appear intermediate between *M. fremontii* s.s. and *M. orbiculatus* (Fig. 33). This PCA shows the Vandenberg specimens to clearly separate from the rest on PC1. PC1 explains 23.6% of the variation with the highest-weighted characters being length of glandular trichomes on the calyx and length of the calyx and calyx lobes (Appendix 2). No additional separation is seen on PC2 (11.9% of the variation), however, both *M. helleri* (including *Sphaeralcea fremontii* var. *exfibulosa*) and the specimens from Shasta County mostly separate from the rest on PC3. PC3 explains 9% of the variation with the highest-weighted characters being the calyx lobe width at widest and at the base as well as length of stellate

trichome rays on the stem. One of the Shasta County specimens plots with *M. howellii* on PC3, however, a separate PCA comparing the Shasta County specimens to *M. howellii* (Fig. 34) clearly divides these two groups along PC1.

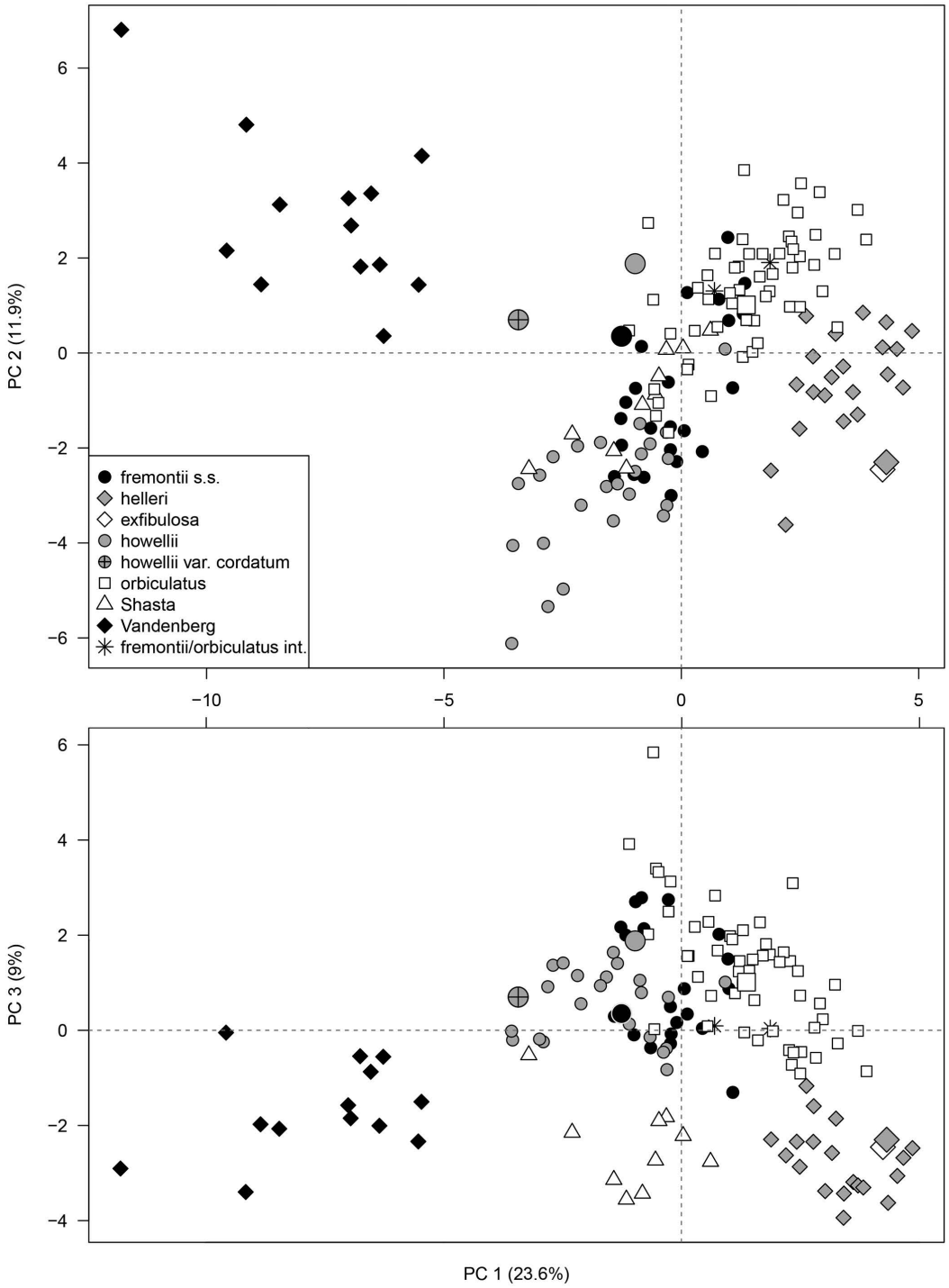

Figure 33. PCA results comparing morphology of groups within *Malacothamnus fremontii* sensu Bates. Larger symbols denote type specimens. Note the type of *Sphaeralcea fremontii* var. *exfibulosa* is mostly hidden behind the type of *M. helleri*.

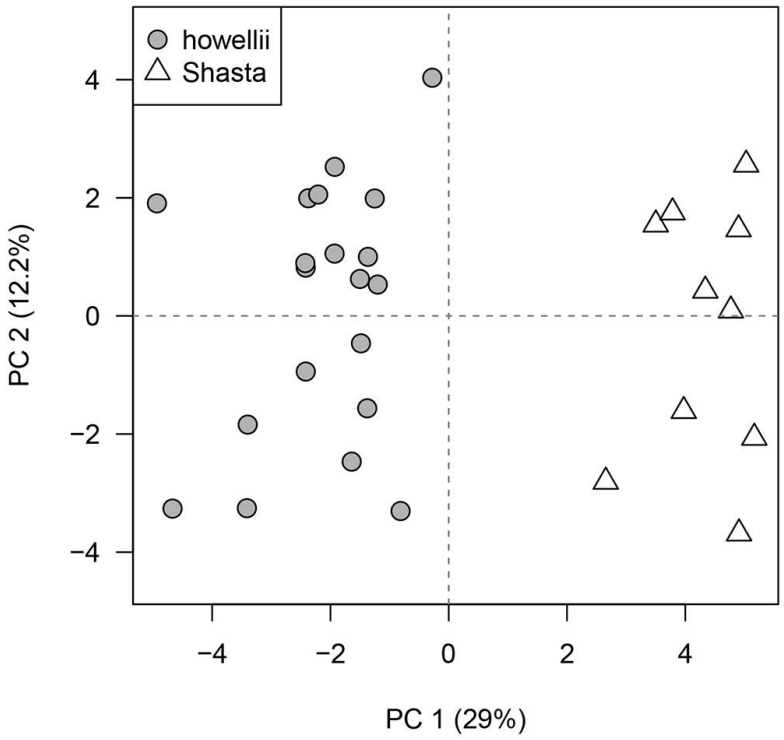

Figure 34. PCA results comparing morphology of *Malacothamnus howellii* to plants from Shasta County.

PCA of *Malacothamnus fremontii* s.s., *M. howellii*, and *M. orbiculatus* shows each grouping to cluster well but with both *M. howellii* and *M. orbiculatus* somewhat overlapping *M. fremontii* s.s. (Fig. 35). *Malacothamnus orbiculatus* can be distinguished from the other two based on the single character of corollas drying closed, whereas *M. fremontii* s.s. and *M. howellii* have the corollas drying open. PCA of just *M. fremontii* s.s. and *M. orbiculatus* improves separation of these groups with only slight overlap (Fig. 36). Two specimens where the ranges of *M. fremontii* s.s. and *M. orbiculatus* come together are morphologically ambiguous suggesting a possible zone of intergradation. PCA appears to support the intermediacy. Five specimens of *M. orbiculatus* cluster together and separate on PC2 based on relatively long and narrow calyx lobes, however, there is no geographic cohesion to these specimens which are scattered across the range of the species.

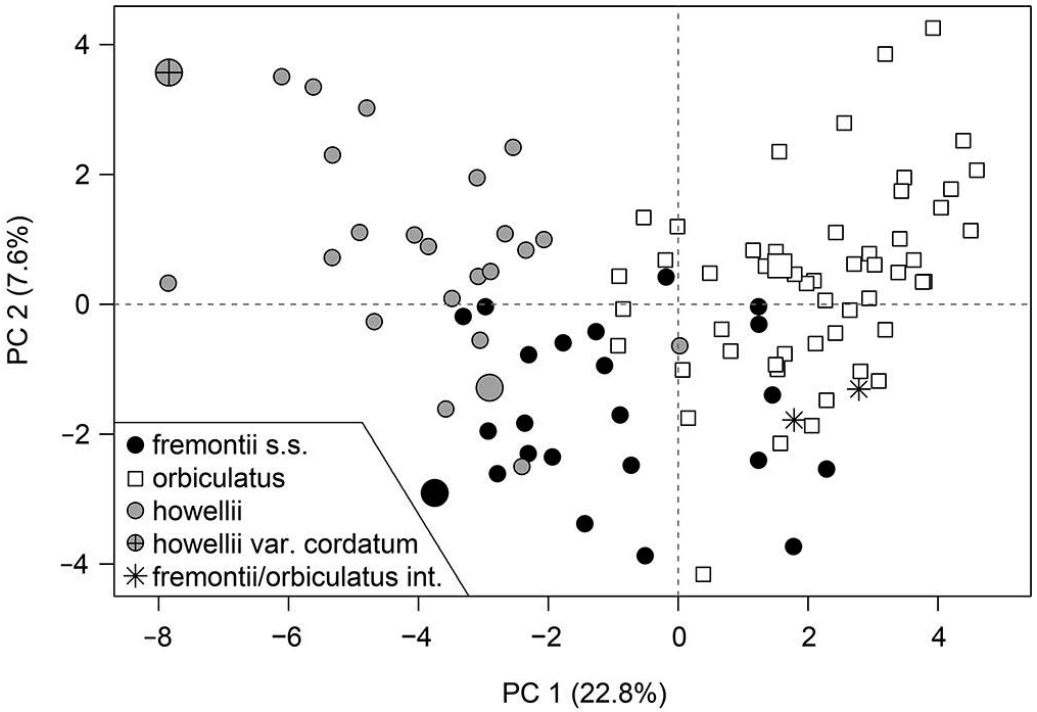

Figure 35. PCA results comparing morphology of *Malacothamnus fremontii* s.s., *M. howellii*, and *M. orbiculatus*. Larger symbols denote type specimens.

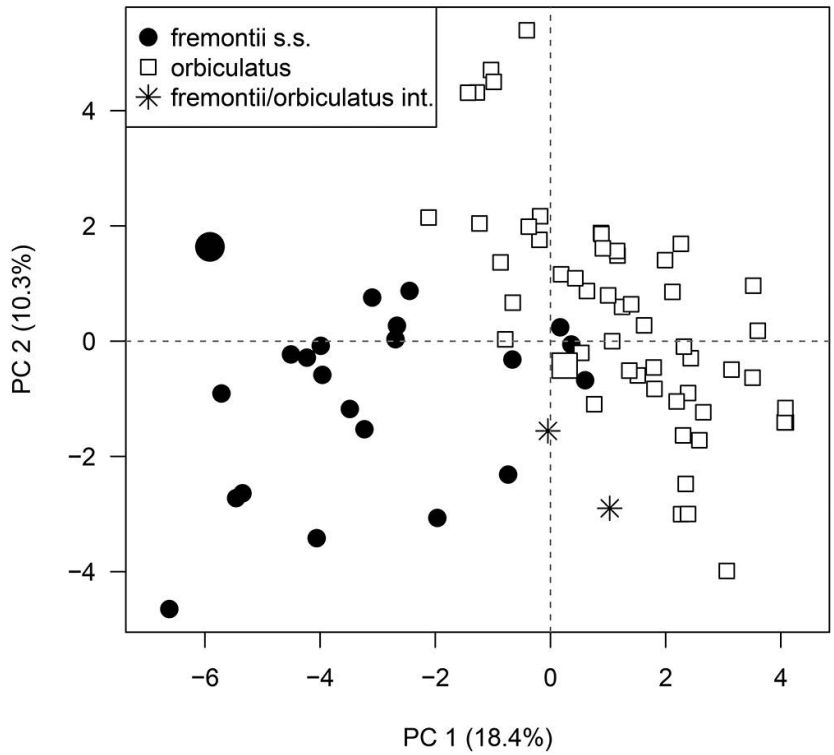

Figure 36. PCA results comparing morphology of *Malacothamnus fremontii* s.s. and *M. orbiculatus*. Larger symbols denote type specimens.

PCA of just *M. orbiculatus*, including the disjunct Arizona specimens, was done to assess possible clustering based on geographic groups (Fig. 37). All geographic regions assessed overlapped in the PCA. No pattern was found comparing Arizona specimens to California specimens. The only geographic pattern found was some specimens from the eastern Transverse Ranges having outliers on both the PC1 and PC2 axes. While interesting that there are outliers in this region, many specimens from this region overlap with the rest of the species in the PCA. One of the major points of confusion with *M. orbiculatus* is how variable it is morphologically. This can possibly be partly attributed to likely hybridization with different taxa across its range (*M. fremontii*, *M. marrubioides*, *M. fasciculatus* var. *laxiflorus*, and *M. fasciculatus* var. *nuttallii*), however, the large spread of points on both the PC1 and PC2 axes for specimens from Arizona, where no other *Malacothamnus* taxa occur to hybridize with, indicate that *M. orbiculatus* may be highly variable morphologically with or without hybridization.

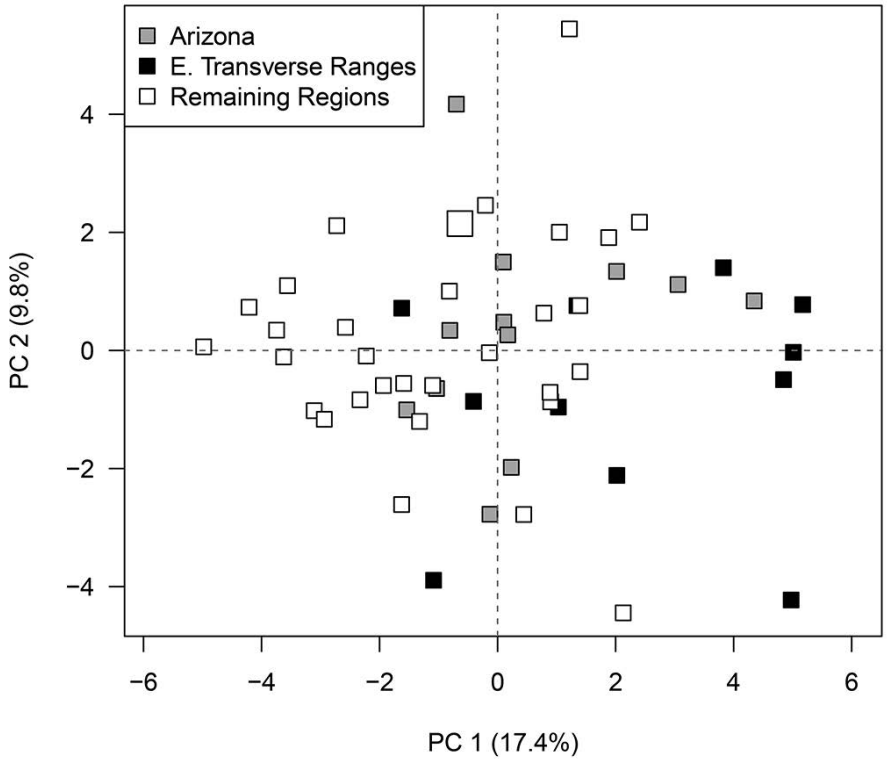

Figure 37. PCA results comparing morphology by geographic region within *Malacothamnus orbiculatus*. The larger square denotes the *M. orbiculatus* lectotype. For clarity, only the Arizona and Eastern Transverse Ranges regions are distinguished from the rest of the species. These are discussed in the text.

PCA of *Malacothamnus fremontii* s.s. and *M. howellii*, with *M. fremontii* s.s. divided into groups growing both north and south of *M. howellii*, shows a relatively clear distinction between *M. howellii* and the southern group of *M. fremontii* s.s. (Fig. 38). This is, however, confounded by the northern group of *M. fremontii* s.s. plotting intermediately. Smaller PC1 values are correlated with larger measurement values of almost all characters. That taken into consideration with geography indicates a possible bidirectional cline (Fig. 39). Plants from the

latitudes of *M. howellii* generally have lower PC1 values than those to the south and plants to the north have similar to higher PC1 values than *M. howellii*. Plants from the longitudes of *M. howellii* separate from those to the south on PC1, but not to the north. From this, it seems logical to assess three possible groups that may or may not be justifiably divided. The *M. howellii* and southern *M. fremontii* s.s. appear mostly distinct with a few possible intermediates. The northern *M. fremontii* s.s. is more problematic as it has plants that could possibly be assigned to either of the other groups. Geographic disjunction of the northern group suggests it could perhaps be distinct genetically from the others. Also problematic is that the type locality of *M. fremontii* is unknown and its PC1 value is somewhat intermediate, though still higher than all from the core *M. howellii* region except for one apparently depauperate specimen. This apparently depauperate specimen raises the question of whether the morphology is related to growing conditions, however, plants grown from seed of both *M. howellii* and southern *M. fremontii* s.s. at California Botanic Garden retained the morphological distinctions of their source populations.

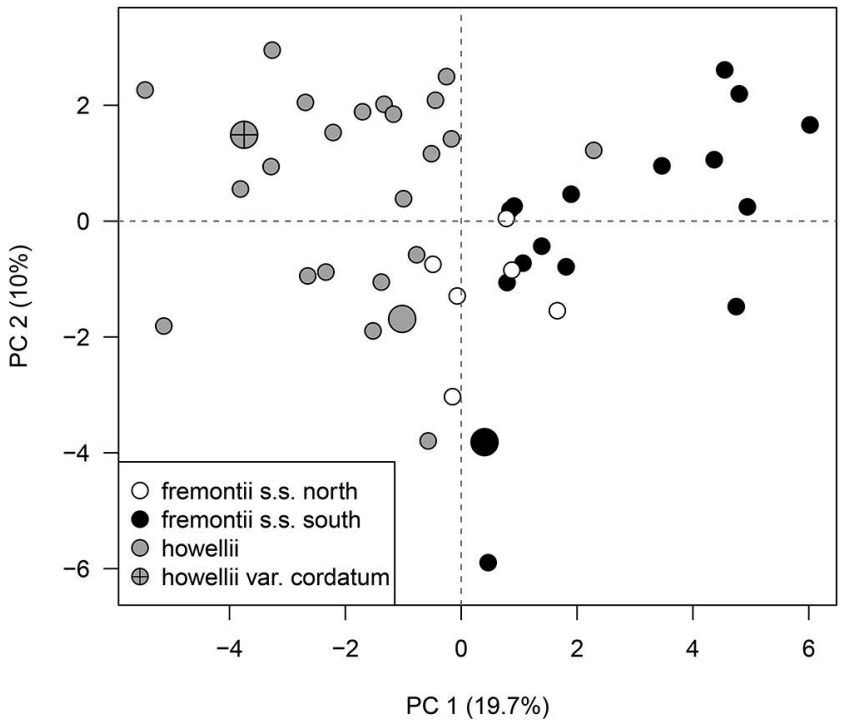

Figure 38. PCA results comparing morphology of the northern and southern regions of *M. fremontii* s.s. to *M. howellii*, which occurs between these regions. Larger symbols denote type specimens.

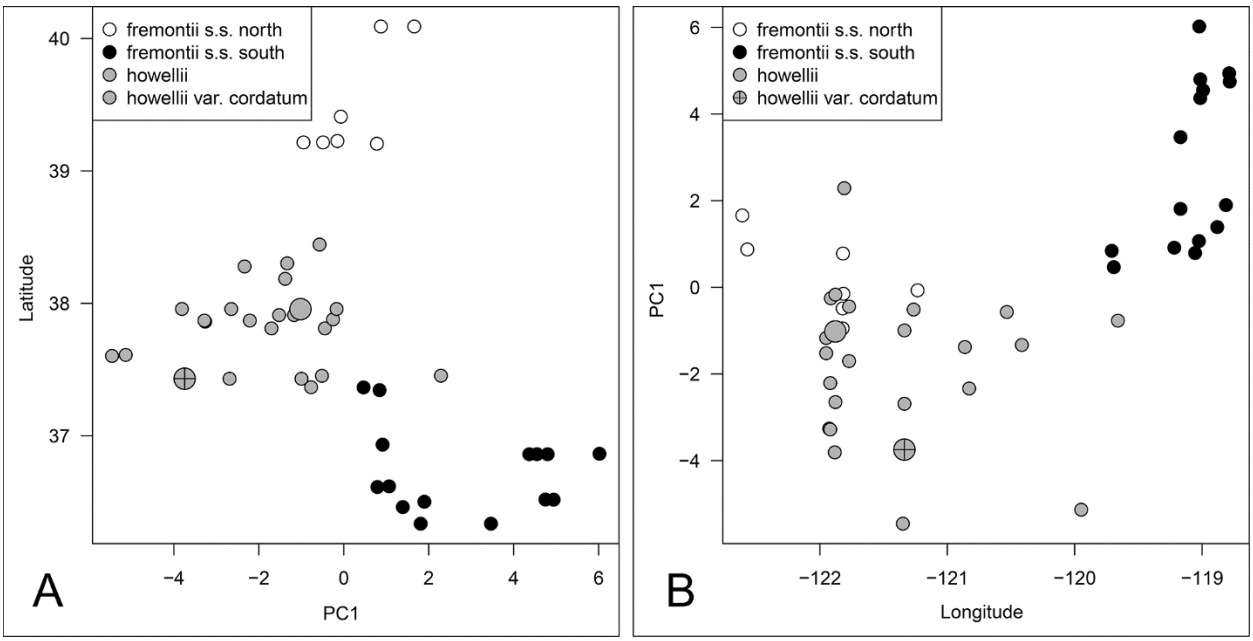

Figure 39. Latitude (A) and longitude (B) plotted against PC1 values from Figure 38. Larger symbols denote type specimens. The *Malacothamnus fremontii* type is not plotted as the collection location is ambiguous.

Attempts to distinguish specimens of *M. howellii* and *M. fremontii* using the key in Kearney (1951) had limited success due to ambiguities in the key. For example, the first part of the couplet is "Calyx (6) 7–8 (10) mm long" for *M. fremontii* vs. "Calyx (8) 9–12 (13) mm long" for *M. howellii*. Of the 46 specimens measured, 50% had a calyx length in the 8–10 mm ambiguous zone. Only one specimen of *M. fremontii* and seven of *M. howellii* are completely unambiguous in the key. That said, if keyed to the best fit, many do fit better with one species or the other. Those from the *M. howellii* region mostly key that direction. Those from the areas north and south of there mostly key in the *M. fremontii* s.s. direction.

Regarding the basionyms Kearney included under *Malacothamnus howellii* (*Malvastrum howellii* var. *howellii, Malvastrum howellii* var. *cordatum,* and *Malvastrum fremontii* var. *cercophorum*), all seem best treated as a single taxon with the varieties of *Malvastrum howellii* interpreted as extreme forms. According to the protolog of *Malvastrum howellii* var. *cordatum*, it is distinguished from the rest of the species by having cordate leaf bases, whereas *Malvastrum howellii* var. *howellii* is supposed to have a truncate leaf base (Eastwood 1936). My study included subcordate within the category cordate when assessing and only found two specimens in *M. howellii* that had no leaves classified as cordate. Examination of images of the type specimens of *M. howellii* suggests the more truncate leaf shape of those specimens may have some genetic influence from *M. hallii*. Putative hybrids between these two species are known from near the *M. howellii* type locality. The type of *Malvastrum fremontii* var. *cercophorum* was not available to fully measure, however, a digital image of the specimen was examined, and it fits well within the rest of what Kearney considered *M. howellii*.

LDA was performed on seven groups including the four clear PCA groupings (*M. helleri*, *M. orbiculatus*, Shasta County specimens, and Vandenberg specimens) and the three less clear

groupings (*M. howellii* and both a northern and southern group of *M. fremontii* s.s.) (Table 12). *Malacothamnus orbiculatus* was classified correctly 100% of the time. *Malacothamnus helleri* and specimens from Shasta County and Vandenberg each had a single misclassification. Similar to the PCA, the remaining three groups were less accurately predicted and perhaps confounded by the northern *M. fremontii* s.s. group or incorrect input classification. In an LDA where the northern and southern groups of *M. fremontii* s.s. are combined (not shown), the prediction accuracy for *M. helleri* increases to 100% and *M. fremontii* s.s. to 97% with no changes in the other groups.

Table 12. Predicted vs. actual group results for LDA of *Malacothamnus fremontii* sensu Bates. Blue with bold numbers indicates a correct prediction and yellow indicates an incorrect prediction.

	Predicted group								
Actual group	fremontii s.s. (north)	fremontii s.s. (south)	howellii	helleri	orbiculatus	"Shasta County"	"Vandenberg"	Total	Percent correctly identified
fremontii s.s. (north)	**5**	1	1	0	0	0	0	7	71%
fremontii s.s. (south)	3	**12**	1	0	0	0	0	16	75%
howellii	2	1	**20**	1	0	0	0	24	92%
helleri	1	0	0	**20**	0	0	0	20	95%
orbiculatus	0	0	0	0	**54**	0	0	54	100%
"Shasta County"	1	0	0	0	0	**9**	0	10	90%
"Vandenberg"	0	0	0	0	1	0	**12**	13	92%

PERMANOVA was run using the same set of specimens and groupings as the first LDA (Table 13). All pairwise comparisons were significant. As seen in other analyses, the pseudo *F*-ratio indicates the comparisons of northern *M. fremontii* s.s. with both *M. howellii* and southern *M. fremontii* s.s. were the least distinct.

Evidence from PCAs, LDA, and PERMANOVA of *Malacothamnus fremontii* sensu Bates indicates at least five distinct groups based on morphology: *M. helleri*, *M. orbiculatus*, the Shasta County specimens, the Vandenberg specimens, and *M. fremontii* (including *M. howellii*). Key characters to distinguish these groups include whether the flowers dry open or closed, width and shape of the calyx, length of stellate trichome rays on the stem, and length of glandular trichomes of the stem and calyx (Table 14). Despite problematic morphological boundaries between *M. fremontii* s.s. and *M. howellii*, their morphologies do follow geographic patterns and their morphological extremes are distinct. This suggests that recognition of *M. howellii* as an infraspecific taxon of *M. fremontii* may be reasonable but should be explored further with DNA analyses to try and clarify if and where taxon boundaries should be drawn. Using only morphological and geographic evidence, all that can be said with much confidence is that *M. howellii* generally has a panicle-like inflorescence and larger calyces and bracts,

whereas *M. fremontii* s.s. generally has a spike-like inflorescence and smaller calyces and bracts. While they cannot be clearly distinguished in these analyses, I retain the northern and southern groups of *M. fremontii* s.s. as well as *M. howellii* for comparison with the full genus as they remain reasonable taxon hypotheses to assess with phylogenetic analyses. All seven retained groups are mapped by PCA symbology to show geographic distribution relative to each other (Fig. 40).

Table 13. PERMANOVA results from pairwise comparisons of morphological groupings in *Malacothamnus fremontii* sensu Bates ordered by pseudo *F*-ratio.

pairs	SumsOfSqs	pseudo-*F*	R^2	*p*-value
helleri vs “Vandenberg”	1.36	80.8	0.72	0.001
howellii vs orbiculatus	1.00	63.3	0.45	0.001
orbiculatus vs “Vandenberg”	0.84	47.2	0.42	0.001
howellii vs “Vandenberg”	0.86	38.4	0.52	0.001
helleri vs “Shasta County”	0.62	36.7	0.56	0.001
helleri vs orbiculatus	0.71	36.3	0.33	0.001
howellii vs “Shasta County”	0.62	30.2	0.49	0.001
helleri vs howellii	0.49	29.0	0.40	0.001
fremontii s.s. (south) vs “Vandenberg”	0.66	28.7	0.51	0.001
“Shasta County” vs “Vandenberg”	0.69	28.6	0.58	0.001
“Shasta County” vs orbiculatus	0.44	25.9	0.29	0.001
fremontii s.s. (south) vs “Shasta County”	0.46	21.2	0.47	0.001
fremontii s.s. (north) vs orbiculatus	0.39	19.7	0.25	0.001
fremontii s.s. (north) vs “Vandenberg”	0.55	19.3	0.52	0.001
fremontii s.s. (south) vs orbiculatus	0.34	18.7	0.22	0.001
fremontii s.s. (north) vs “Shasta County”	0.40	16.2	0.52	0.001
fremontii s.s. (south) vs helleri	0.32	15.6	0.31	0.001
fremontii s.s. (south) vs howellii	0.27	12.6	0.25	0.001
fremontii s.s. (north) vs helleri	0.24	12.0	0.32	0.001
fremontii s.s. (south) vs fremontii s.s. (north)	0.14	4.9	0.19	0.001
fremontii s.s. (north) vs howellii	0.11	4.4	0.13	0.001

Table 14. Characters useful in distinguishing the five morphologically distinct groups within *M. fremontii* sensu Bates. Character measurements in bold indicate the combination of characters that distinguish each group from the rest.

Taxon	Calyx lobe width	Calyx lobe width at widest/ width at base	Corollas drying	Longest glandular trichome length calyx	Longest glandular trichome length stem	Mean stellate trichome length stem	Leaf base
"Shasta County"	**5–7 mm**	**1.4–3**	Somewhat open	0	0	0.2–0.4 mm	Generally cordate
"Vandenberg"	2.5–4 mm	1–1.3	**Closed**	**0.4–0.9 mm**	**0.3–0.8 mm**	0.4–0.8 mm	Generally cordate
M. orbiculatus	1.5–3.5 mm	0.8–1.3	**Closed**	**0–0.1 mm**	**0**	0.2–0.6(0.9) mm	Generally cordate
M. helleri	2–3.5 mm	1–1.3	**Open**	0–0.1 mm	0	**0.1–0.3(0.4) mm**	**Generally truncate to cuneate**
M. fremontii (+ *M. howellii*)	2–4.5(5) mm	1–1.2	**Open**	0–0.4 mm	0–0.1 mm	**(0.3)0.4–0.7 mm**	**Generally cordate**

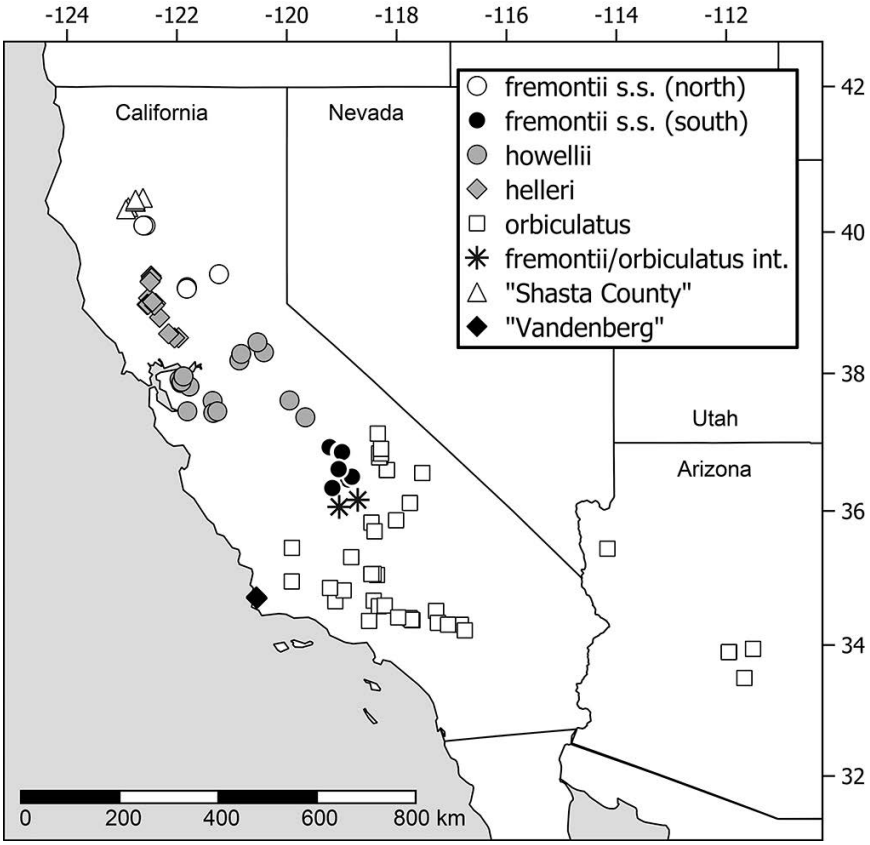

Figure 40. *Malacothamnus fremontii* sensu Bates mapped using symbology from PCAs. Circles indicate *M. fremontii* s.s. and *M. howellii*, which are perhaps best treated as only one or two groups, rather than the three shown, and need phylogenetic analyses to clarify if and where taxon boundaries in this group should be delineated.

3.7 *Malacothamnus jonesii* sensu Bates and *M. abbottii*

Malacothamnus jonesii sensu Bates is distinguished from all other *Malacothamnus* species by the combination of narrow and often red calyx bracts, calyces that are not angled or winged in bud, dense stellate trichomes, relatively small leaves, and by having less than six flowers clustered at each inflorescence node (Bates 1963, 2015). The morphologically similar *M. abbottii* is distinguished from the rest of the genus by the combination of relatively wide (1-1.5 mm) linear calyx bracts and a panicle-like inflorescence. *Malacothamnus jonesii* sensu Bates and *M. abbottii* are assessed using PCA, LDA, and PERMANOVA to clarify finer-scale morphological groupings within *M. jonesii* sensu Bates and how similar they are to *M. abbottii*.

Four basionyms are included under *Malacothamnus jonesii* sensu Bates (Fig. 1), which were treated as *M. jonesii* s.s*., M. gracilis,* and *M. niveus* by Kearney (1951). The basionym *Malvastrum dudleyi* has been considered a synonym of *M. jonesii* s.s. in all treatments since the original circumscription. Eastwood (1936a) distinguished *Malvastrum dudleyi* from *M. jonesii* s.s. with "Leaves truncate at base, crenate" for *M. jonesii* s.s. and "Leaves cuneate at base, irregularly dentate" for *Malvastrum dudleyi*. The type locality of *Malvastrum dudleyi* is just 3 km west of the type locality of *M. jonesii* in Paso Robles, CA. This close distance indicates that differences between *Malvastrum dudleyi* and *M. jonesii* s.s. may just be variation within a single species. Bates (1963) notes in his treatment combining the four basionyms that *M. jonesii* sensu Bates "although heterogenous in its most extreme forms, has an over-all continuity both morphologically and geographically". After a description of these extreme forms, he notes plants and populations throughout the range of *M. jonesii* sensu Bates that are "scarcely characteristic" of these and suggests they are best included in a single taxon. Sampling for analyses includes four morphologically and geographically intermediate specimens: two intermediates between *M. niveus* and *M*. *gracilis*, and two intermediates between *M. niveus* and *M. jonesii* (Fig. 41).

Malacothamnus abbottii is uncontested as a distinct species. Vegetatively it is very similar to *M. jonesii* sensu Bates and its range is closely adjacent to that of *M. jonesii* s.s. This argues for *M. abbottii* being possibly closely related to *M. jonesii* sensu Bates. *M. abbottii* is, however, easily distinguished from the rest in flower by its wider calyx bracts and, while its blooming period overlaps with *M. gracilis*, it does not flower at the same time as *M. jonesii* s.s., the only one of this group it is known to naturally occur near. I've included *M. abbottii* in some *M. jonesii* sensu Bates analyses to compare how distinct this similar species is to each of the species treated within *M. jonesii* sensu Bates.

A PCA of *Malacothamnus jonesii* sensu Bates with *M. abbottii* shows four clusters with little overlap corresponding to *M. abbottii*, *M. gracilis*, *M. jonesii* s.s., and *M. niveus* (Fig. 42). *Malvastrum dudleyi* plots within the variation of *M. jonesii* s.s. PC1 explains 22.3% of the variation and mostly separates *M. abbottii*, *M. gracilis*, and *M. jonesii* s.s. with the highest-weighted characters being calyx glandular trichome length, calyx lobe length, and calyx bract width (Appendix 2). PC2 explains 19.1% of the variation and separates *M. niveus* from *M. jonesii* s.s. and *M. gracilis* with the highest-weighted characters being stellate trichome ray length on the calyx and stem.

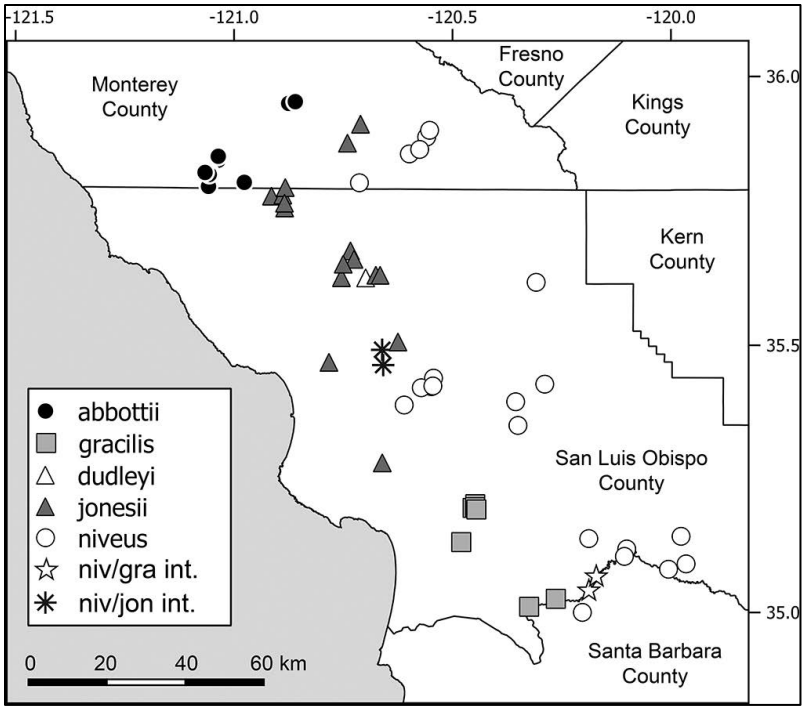

Figure 41. Map showing the geographic distribution of specimens sampled within *M. abbottii* and *M. jonesii* sensu Bates including apparent intermediates of *M. niveus* with both *M. gracilis* and *M. jonesii* s.s.

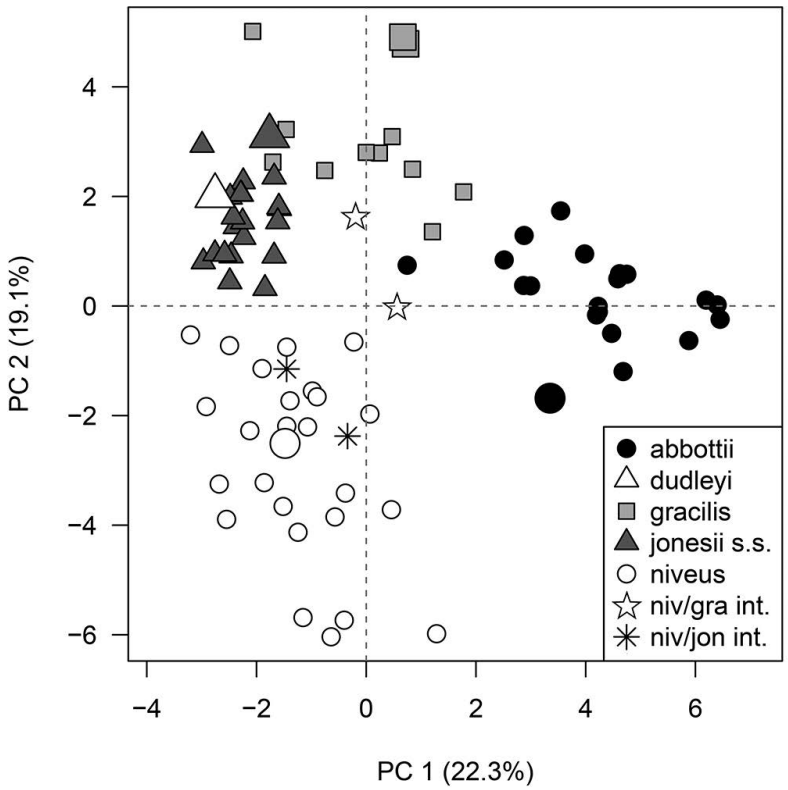

Figure 42. PCA results comparing morphology of *Malacothamnus abbottii* and species within *M. jonesii* sensu Bates including apparent intermediates of *M. niveus* with both *M. gracilis* and *M. jonesii* s.s. Larger symbols denote type specimens.

A PCA of just *Malacothamnus jonesii* sensu Bates with possible intermediate specimens shows improved clustering with no overlap between *M. gracilis*, *M. jonesii* s.s., and *M. niveus* (Fig. 43). The two possible *M. gracilis/niveus* intermediates plot intermediately as expected, though each could arguably be assigned as an extreme form to one of the species. The two possible *M. jonesii/niveus* intermediates plot within the variation of *M. niveus*. *Malvastrum dudleyi* again plots within the variation of *M. jonesii* s.s. PC1 explains 26.3% of the variation and separates *M. niveus* from the other two species with the highest-weighted characters again being stellate trichome ray length on the calyx and stem (Appendix 2). PC2 explains 13.3% of the variation and separates *M. gracilis* from *M. jonesii* s.s. with the highest-weighted characters being inflorescence type and branch length, calyx lobe distance from tip where 1 mm wide, and calyx glandular trichome length.

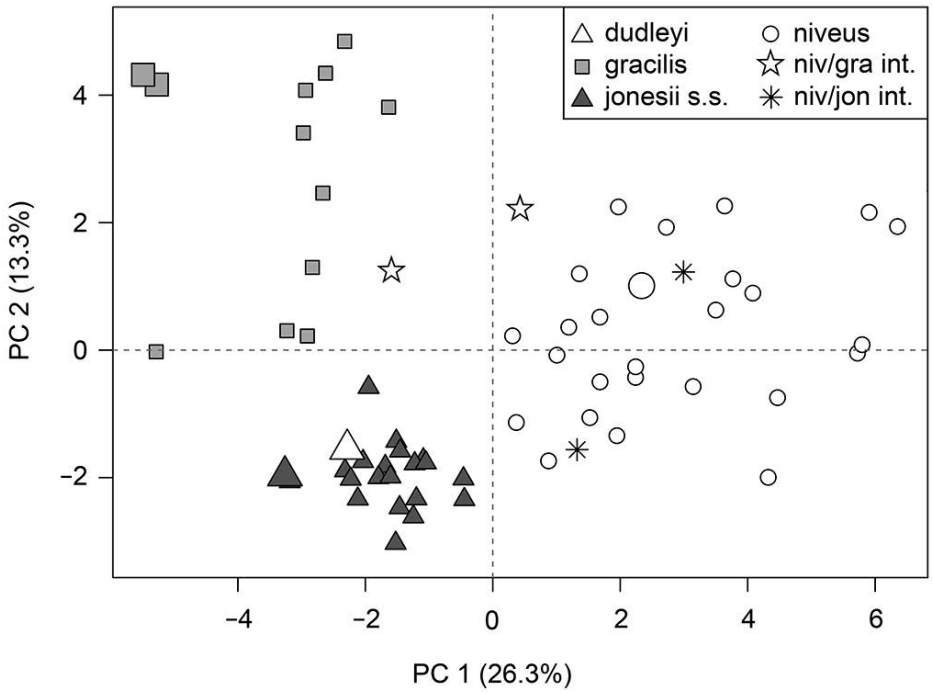

Figure 43. PCA results comparing morphology of species within *M. jonesii* sensu Bates including apparent intermediates of *M. niveus* with both *M. gracilis* and *M. jonesii* s.s. Larger symbols denote type specimens.

LDA was run using all specimens with four groups based on PCA clustering: *Malacothamnus abbottii*, *M. gracilis*, *M. jonesii* s.s., and *M. niveus* (Table 15). *Malvastrum dudleyi* was assigned to *M. jonesii* s.s., the possible *M. jonesii/niveus* intermediates were assigned to *M. niveus*, and each of the possible *M. gracilis/niveus* intermediates were assigned to their closest PCA cluster as either *M. gracilis* or *M. niveus*. Only four specimens were misclassified in this analysis, three of which were previous noted as likely being intermediates. The two *M. jonesii/niveus* intermediates that clustered with *M. niveus* in the PCA were identified as *M. jonesii* s.s. in the LDA. One of the *M. gracilis/niveus* intermediates was also identified as *M. jonesii* s.s. The final misidentification was of a *M. gracilis* specimen with an atypical spike-like inflorescence. This was identified as *M. jonesii* s.s., which typically has spike-

like inflorescences. A separate LDA was run with no suspected intermediates (not shown). This LDA had 100% correct identification with the exception of the *M. gracilis* specimen with a spike-like inflorescence again being misclassified as *M. jonesii* s.s.

PERMANOVA was run using the same set of specimens and groupings as the LDA excluding the four intermediate specimens as they could not be clearly assigned to a particular group (Table 16). All pairwise comparisons were significant. The pseudo *F*-ratio indicates *Malacothamnus abbottii* vs. *M. jonesii* is the most distinct of these comparisons and *M. abbottii* vs. *M. gracilis* was the least distinct. Comparisons with the clear species *M. abbottii* were not much different than between groups within *M. jonesii* sensu Bates, however, removing the intermediates likely skews those comparisons somewhat.

Evidence from PCAs, LDA, and PERMANOVA of *Malacothamnus abbottii* and *M. jonesii* sensu Bates indicates four morphological groups: *M. abbottii*, *M. gracilis*, *M. jonesii* s.s., and *M. niveus*. *Malvastrum dudleyi* appears to have been correctly treated as a synonym of *M. jonesii* based on PCA. No intermediates with *M. abbottii* were found but morphological intermediates in geographically intermediate areas between *M. niveus* and both *M. jonesii* and *M. gracilis* indicates possible intergradation between species within *M. jonesii* sensu Bates. Table 17 indicates useful characters to distinguish between *M. abbottii*, *M. gracilis*, *M. jonesii* s.s., and *M. niveus*. This generally follows the distinctions of Kearney (1951).

Table 15. Predicted vs. actual group results for LDA of *Malacothamnus abbottii* and *M. jonesii* sensu Bates. Blue with bold numbers indicates a correct prediction and yellow indicates an incorrect prediction. Note that three of the four misidentifications are suspected intermediates.

	Predicted group					
Actual Group	abbottii	gracilis	jonesii s.s.	niveus	Total	Percent correctly identified
abbottii	**20**	0	0	0	20	100%
gracilis	0	**11**	2	0	13	85%
jonesii s.s.	0	0	**22**	0	22	100%
niveus	0	0	2	**27**	29	93%

Table 16. PERMANOVA results from pairwise comparisons of morphological groupings in *Malacothamnus abbottii and M. jonesii* sensu Bates

Pairs	**SumsOfSqs**	**pseudo-*F***	**R^2**	***p*-value**
abbottii vs jonesii	1.07	39.4	0.50	0.001
abbottii vs niveus	0.86	32.2	0.42	0.001
gracilis vs niveus	0.70	25.9	0.42	0.001
jonesii vs niveus	0.59	24.1	0.34	0.001
gracilis vs jonesii	0.56	18.5	0.37	0.001
abbottii vs gracilis	0.59	17.3	0.37	0.001

Table 17. Characters useful in distinguishing *M. abbottii* and the three species within *M. jonesii* sensu Bates. Character measurements in bold indicate characters that distinguish each species from the rest.

Taxon	Mean stellate trichome ray length on calyx	Inflorescence type	Calyx bract width	Calyx bract color
M. niveus	**0.5–0.8 mm**	Panicle-like (rarely spike-like)	0.3–0.7(1.4) mm	Reddish, rarely green
M. jonesii	0.2–0.4 mm	**Spike-like**	0.2–0.7 mm	Reddish, rarely green
M. abbottii	0.1–0.2 mm	Panicle-like (rarely spike-like)	**0.5–1.8 mm**	**Green, rarely reddish**
M. gracilis	0.1–0.3 mm	Panicle-like (rarely spike-like)	0.2–0.6 mm	Reddish

3.8 Full Genus Comparisons

After assessing the species subsets for finer-scale morphological groupings, the final groupings from each of these subsets were used in full genus comparisons. Thirty-eight morphological groupings were retained from the previous analyses. These mostly follow the taxa of Kearney (1951, 1955) but with additional groupings hypothesized in this study. For ease of comparison between these finer groupings and the broader Bates groupings, morphological groupings in figures are shown as subgroups of the 11 Bates (2015) groupings plus the recently described *M. enigmaticus* as a 12th grouping.

PCAs run on the full genus resolved the same morphological groupings as those found in the previous PCAs. The primary difference in running PCAs starting with the entire dataset rather than with subsets was the order in which the morphological groups separated out. Many taxa and other morphological groups did not cluster with the taxa Bates synonymized them with, which indicates that some of the broader groupings of Bates (2015) are questionable. The only novel grouping of taxa to come out of these PCAs was a cluster of *Malacothamnus arcuatus* (*M. fasciculatus* sensu Bates) and *M. helleri* (*M. fremontii* sensu Bates) with *M. jonesii* and *M. niveus* (*M. jonesii* sensu Bates), all of which separated in further PCAs.

LDA was run on the full genus (Table 18). Of the 38 morphological groups included, six were correctly assigned 100% of the time, 17 at least 90% of the time, and 28 at least 75% of the time. All but one of those groups with less than 75% correctly assigned specimens belong to *Malacothamnus fasciculatus* sensu Bates. The other is due to misclassification between the two geographic areas of *M. davidsonii*. Incorrect assignments mostly follow those of the subset LDAs. Most incorrect assignments between groups not compared in subsets are as expected. For example, four *M. davidsonii* were incorrectly assigned to *M. orbiculatus* and two *M. orbiculatus* to *M. davidsonii*. Some plants of *M. orbiculatus* do look quite similar to *M. davidsonii* but they can generally be easily distinguished by the size and shape of full plants, which cannot be assessed from the material on herbarium specimens. The only assignments that stood out as odd are three specimens of *M. abbottii* assigned to *M. parishii*. This is likely due to very low sampling of *M. parishii*.

PERMANOVA was run on the full genus to assess significance of pairwise comparisons between groups not accounted for in previous PERMANOVAs (Appendix 3). Of the 703 pairwise

comparisons, only 17 had a *p*-value of ≥ 0.01. Of these 17 comparisons, 14 included the "Santa Rosa Mountains" group, which only had two specimens measured, and the remaining three included *M. parishii*, which only had three specimens measured. Poor sampling of these two groups may at least partly account for these insignificant *p*-values.

Table 18. LDA assessing the full genus *Malacothamnus* classified by the 38 morphological groups recovered in species subset analyses. Narrow black lines divide the table into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group. Blue indicates correct assignment. Yellow indicates an incorrect assignment to the finer scale morphological grouping but correct assignment within a Bates species. Red indicates an incorrect assignment to both the finer scaler grouping and Bates species.

Predicted group (this row) / Actual group (this column)	**enigmaticus**	"Baja E"	"Baja E"/fasciculatus int.	fasciculatus/foliosus int.	**fasciculatus s.s.**	catalinensis	"Santa Rosa Mtns"	laxiflorus	nesioticus	nuttallii	parishii	mendocinensis	hallii	arcuatus	davidsonii (north)	**davidsonii (south)**	**abbottii**	gracilis	niveus	**jonesii**	helleri	howellii	**fremontii (south)**	fremontii (north)	"Shasta County"	"Vandenberg"	orbiculatus	**clementinus**	viscidus	densiflorus (SD + SA)	**densiflorus (SJ)**	foliosus (coastal)	**foliosus (inland)**	**marrubioides**	**aboriginum**	involucratus	**palmeri**	lucianus	Total samples	Total correct	% correct
enigmaticus	18	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	20	18	90
"Baja E"	2	2	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	2	33
"Baja E"/fasciculatus int.	0	0	4	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	4	57
fasciculatus/foliosus int.	0	0	3	10	2	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	10	53
fasciculatus s.s.	0	1	0	0	26	2	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32	26	81
catalinensis	0	0	0	0	1	18	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	18	86
"Santa Rosa Mtns"	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	50
laxiflorus	0	2	0	0	3	3	0	40	2	3	0	1	3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	40	69
nesioticus	0	0	0	1	0	0	0	1	8	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	8	62
nuttallii	0	0	0	0	0	0	0	6	0	15	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	15	68
parishii	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	100
mendocinensis	0	0	0	0	0	0	0	2	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	3	60
hallii	0	0	0	0	1	1	0	4	0	1	0	0	20	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29	20	69
arcuatus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	22	96
davidsonii (north)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	19	16	84
davidsonii (south)	0	0	0	1	0	0	0	1	1	0	0	0	0	0	5	15	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	24	15	63
abbottii	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	20	15	75
gracilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	10	83
niveus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26	24	92
jonesii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	22	100
helleri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	21	100
howellii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	21	88
fremontii (south)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	13	81
fremontii (north)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	6	86
"Shasta County"	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	10	9	90
"Vandenberg"	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	13	13	100
orbiculatus	0	1	0	0	1	0	0	2	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	46	2	0	0	0	1	0	0	0	0	0	0	55	46	84
clementinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	19	0	0	0	0	0	0	0	0	0	0	20	19	95
viscidus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	18	0	0	0	0	0	0	0	0	0	20	18	90
densiflorus (SD + SA)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	25	1	0	0	0	0	0	0	0	27	25	93
densiflorus (SJ)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	9	0	0	0	0	0	0	0	11	9	82
foliosus (coastal)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	3	0	0	0	0	0	17	14	82
foliosus (inland)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	17	16	94
marrubioides	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	0	0	0	0	21	19	90
aboriginum	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	18	0	0	0	20	18	90
involucratus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	31	1	0	34	31	91
palmeri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	0	24	24	100
lucianus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	22	22	100

A morphological distance matrix was used to assess similarity between all morphological groupings in the genus (Fig. 44). This matrix shows distance between group centroids calculated using pairwise Spearman correlation distance between all samples measured. Groupings found most similar in the distance matrix generally follow the findings of the previous analyses. One of the starkest contrasts between subsets analyzed is that the three morphological groups with the longest glandular trichomes (*M. lucianus*, *M. densiflorus* var. *viscidus*, and the Vandenberg plants) are more similar to each other than to those they were grouped with by Bates. These

three groups are quite distinct from each other as well as evidenced by only a single misclassification between them in the LDA of the full genus. Also notable is that while many of the finer scale morphological groupings are most similar to other groupings within the same Bates species, *M. fremontii* sensu Bates clearly does not form a morphologically cohesive group.

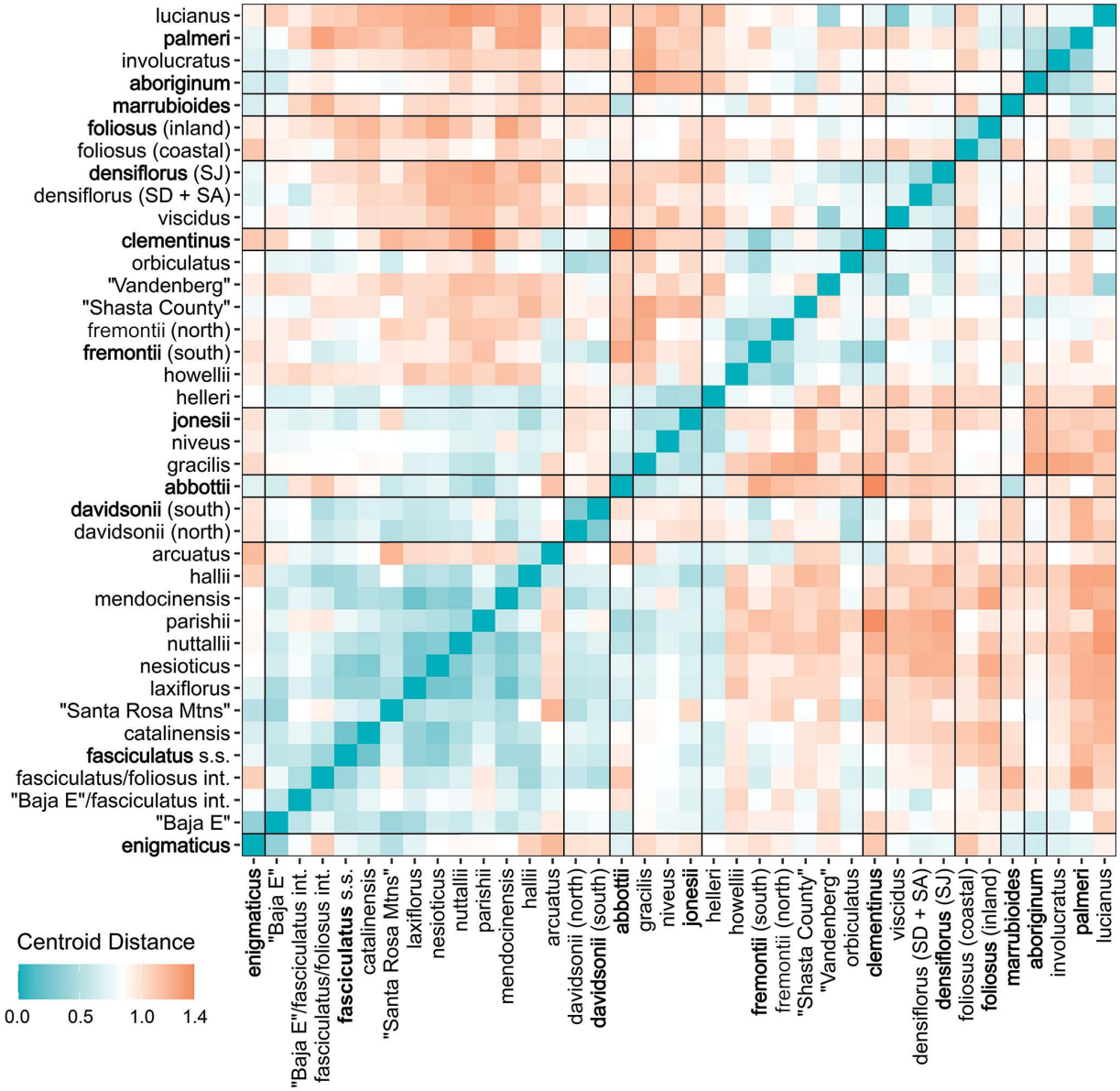

Figure 44. Heat-map based on Spearman correlation distance derived from comparative morphological data of *Malacothamnus* specimens. Darker blues indicate morphological groupings that are more similar and darker reds indicate groupings that are more dissimilar. Black lines divide the matrix into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

4 UTILITY OF MEASURED CHARACTERS IN DISTINGUISHING TAXA

The following summarizes the morphological characters assessed in this study and which of these are most useful in distinguishing taxa. While very few characters are distinct for any particular *Malacothamnus* taxon and many characters are variable or overlap, combinations of characters are very effective in distinguishing many taxa and other morphological groupings subsumed into the broadly defined species of Bates. Key morphological characters include inflorescence type, calyx and calyx bracts (especially in combination), stipular bracts, length of stellate trichome rays, density of stellate trichomes, length of glandular trichomes, and leaf shape. Figures showing measurements of the most useful characters are included in the main text and those less useful as well as some with redundant patterns are included as supplemental figures at the end of this volume in Appendix 4.

4.1 Inflorescence

Four inflorescence characters were measured: the position and length of the longest inflorescence internode, the longest inflorescence branch length, and the inflorescence type. Of these, the qualitative character of inflorescence type is probably the most useful in distinguishing taxa. Inflorescences are cymose and vary in flower arrangement from capitate to spike-like to panicle-like, sometimes grading from one to another in the same population (Bates 1963). While there are taxa that vary considerably, several can be generally classified to a single inflorescence type. Of the quantitative characters measured, the longest inflorescence branch length best shows inflorescence type and variation with the exception that it does not distinguish those with capitate inflorescences from those that are spike-like. Longest inflorescence branch length may also not well represent some generally spike-like inflorescences with axillary spikes at the proximal end of the inflorescence. Figure 45A shows boxplots of the longest inflorescence branch length and Fig. 45B shows the proportion of each inflorescence type within each morphological group. While inflorescence type can be very useful in distinguishing between some groups, Fig. 45B illustrates how variation in inflorescence types within a group can limit its utility as a clear divider between others. Position and length of the longest inflorescence internode primarily differentiated those specimens with capitate inflorescences from the rest as those with capitate inflorescences were assigned a value of zero in these two categories (Figs S1 and S2). In most specimens, the most proximal inflorescence internode was the longest.

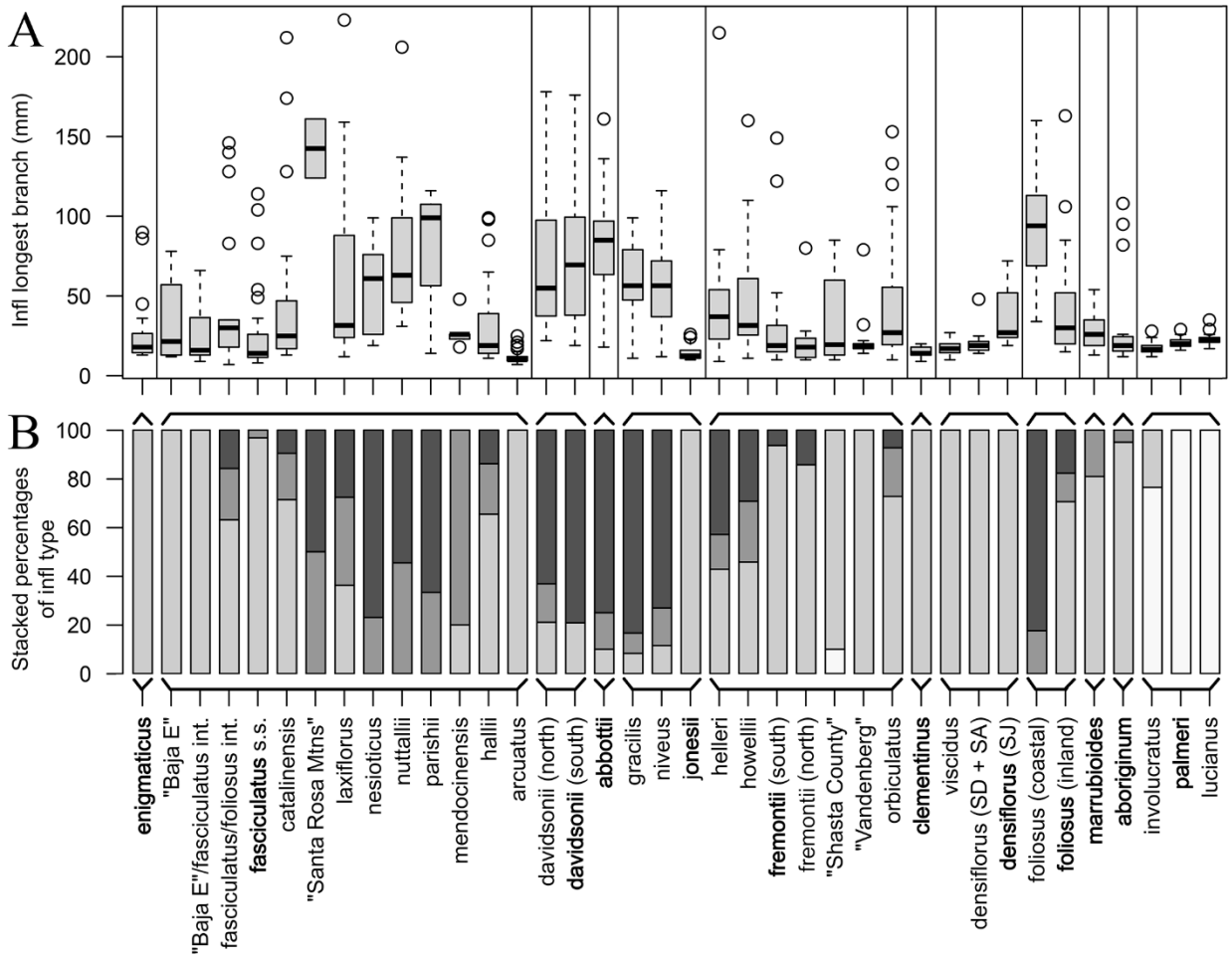

Figure 45. A) Boxplots comparing longest inflorescence branch length between final morphological groupings. B) Stacked barplots showing the proportion of inflorescence types within morphological groupings. Inflorescence type: capitate to subcapitate (white), spike-like (light grey), borderline spike/narrow panicle (medium grey), wide panicle (dark grey). Vertical lines (A) and brackets (B) divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

4.2 Corolla

Whether corollas dry open or closed is a key character in differentiating a few taxa from the rest. Almost all taxa have corollas drying closed, with five of those having an outlier that was partly open and one with an outlier fully open (Fig. 46). Three species treated under *M. fremontii* by Bates (*M. fremontii* s.s., *M. helleri*, and *M. howellii*) had corollas always or mostly drying fully open. *Malacothamnus fremontii* s.s. and *M. howellii* are clearly related and may not be distinct. *Malacothamnus helleri*, may also be closely related to these two taxa based on the common character state of corollas drying open as well as having an adjacent geographic range. The only other group to have corollas drying fully open were the plants from Shasta County, however, these mostly had corollas drying partially rather than fully open.

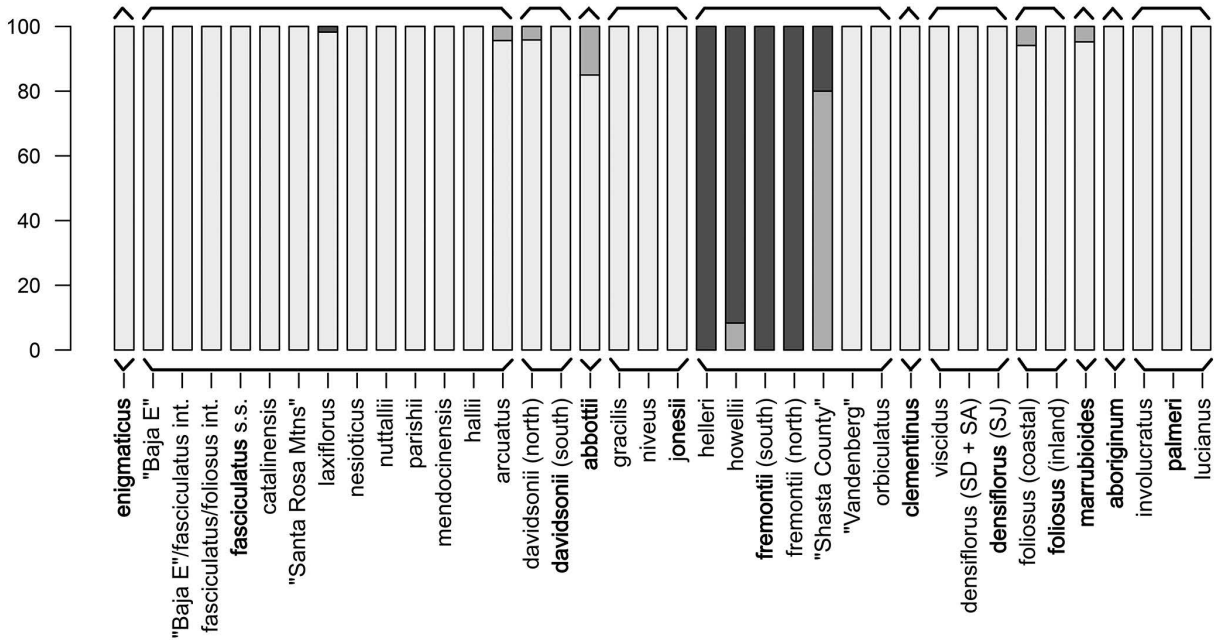

Figure 46. Stacked barplots showing the proportion of specimens with each drying corolla character state within the final morphological groupings. Drying corolla character state: drying closed (pale grey), drying somewhat open (medium grey), drying fully open (dark grey). Brackets divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

4.3 Calyx

Six characters were used to quantify the shape of the calyx. The combination of calyx length and calyx lobe length also accounts for the length of the calyx tube. Shape of the calyx lobes was accounted for with two width measures (the widest area and at the base), distance from the center of the base to the center of the widest area, and distance from the distal end of the calyx lobe to the center of where it expands to 1 mm wide. Calyx length shows clear differences between some morphological groupings (Fig. 47A). Calyx lobe length (Fig. S3) and distance from the distal end of the calyx lobe to where it is 1 mm wide (Fig. S4) mostly follow the plotted pattern of calyx length in Figure 47A.

The ratio of calyx width at widest to width at base (ratio in Fig. 47B and individual measurements in Figs. S5 and S6) prominently separates three morphological groupings that have lobes much wider above the base, whereas the calyx lobes of others are generally widest at the base itself or the difference between measures is much less distinct. The morphological groups with the calyx lobe much wider above the base include *M. aboriginum*, *M. foliosus* sensu Bates (particularly the more coastal ones generally assigned to *M. paniculatus*), and the plants from Shasta County. Note that this is a strong character differentiating the Shasta County plants from *M. fremontii* sensu Bates in which it has been previously included.

Distance from the base of the calyx lobe to the widest area (Fig. S7) distinguishes those groups where the calyx is widest at the base from the rest, though many of these groups have some outliers with values similar to other taxa.

While the character of ridges on the veins of the calyx showed patterns following those of some other characters (Fig. S8), I found it to be a dubious character to assess. It was unclear in many specimens whether these ridges are an actual ridge present before drying or if the ridge was a result of the way that particular calyx dried. Likewise, how much the ridge protruded could be a result of the way the calyx dried. Of the three character states recorded (no ridge, slightly protruding, and obviously protruding), all morphological groupings had at least one specimen in the intermediate category of slightly protruding and only *M. palmeri* edged toward obviously protruding. A more appropriate assessment of this character would be to examine the anatomy of the ridge in cross-sections of the calyx, but I see little to no utility in this as other characters appear to be much more useful in distinguishing the morphological groupings.

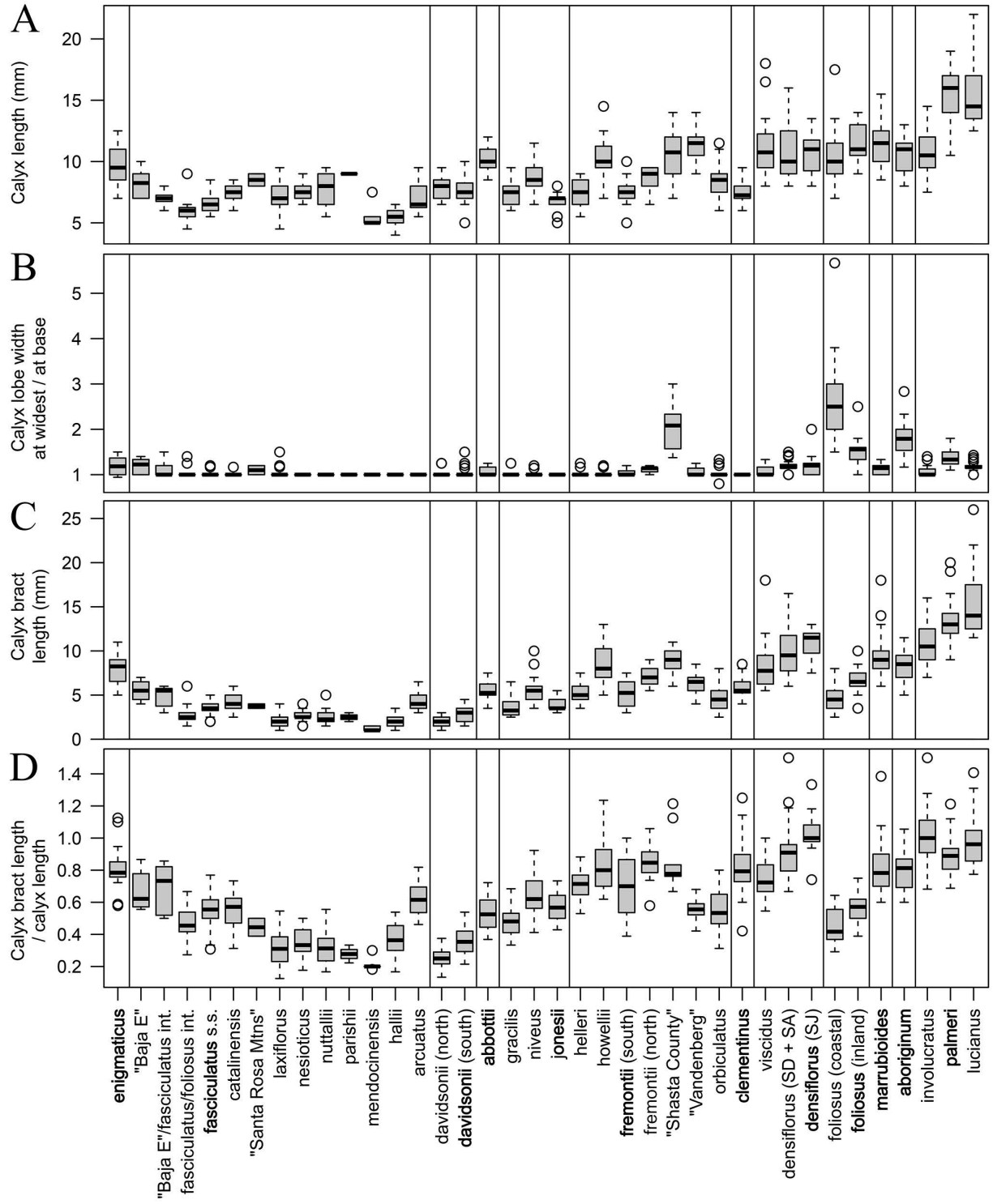

Figure 47: Boxplots comparing calyx and calyx bract characters between morphological groupings: A) Length of calyx. B) Ratio of the calyx lobe width at the widest point to the width at the base of the lobe. C) Calyx bract length. D) Ratio of the calyx bract length to the calyx length. Vertical lines divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

4.4 Bracts

Length and width of calyx bracts were measured. Both the calyx bract length and the ratio of the length of the calyx bracts to the calyx have been used to distinguish *M. fasciculatus* sensu Bates and *M. davidsonii* from the rest of the genus as these species have relatively short calyx bracts and the length of these bracts is generally a smaller proportion of the full calyx length (Fig. 47C and D). While these characters overlap between many groups, the utility of these characters is evident in distinguishing between those that do not.

Excluding *M. palmeri* sensu Bates, which is easily distinguished in other ways, calyx bract width distinguishes two species from the rest of the genus: *M. abbottii* and *M. aboriginum* (Fig. 48B). *Malacothamnus aboriginum* is distinctive in having relatively wide calyx bracts with a width that is often half or more the length of the bract. In *M. aboriginum*, these bracts are also occasionally connate, which is not seen in the rest of the genus. *Malacothamnus abbottii* has linear bracts like much of rest of the genus, however, these linear bracts are relatively wide giving them a stouter appearance than similar taxa. The three species in *M. palmeri* sensu Bates also have wider calyx bracts but are easily distinguished from the rest of the genus based on generally having a capitate to subcapitate inflorescence in combination with other characters.

Both Kearney (1951) and Slotta (2012) include calyx bract color in their keys to the genus. Kearney refers to dark bracts and Slotta refers to bracts turning black in age. In both cases these are attributed to species in *M. jonesii* sensu Bates. Examination of specimens shows the darker/black bracts to be red, sometimes very dark red and appearing black, whereas green is the alternative color. As some bracts are both red and green, three categories were used to assess this character: “green”, “partially red/black”, and “all or mostly red/black”. Figure 48A shows the relative abundance of these categories in each of the morphological groups. Worth noting is that some red was observed in most groups and is likely possible in all groups. There are, however, groups where the red coloration is either very common or rare/absent, which is particularly useful in similar groups such as *M. abbottii* vs. *M. gracilis* and *M. densiflorus* var. *viscidus* vs. the Vandenberg plants. Note that *M. gracilis* is the only morphological group to predominantly fit in the category “all or mostly red/black”.

The length and width of the widest stipular bract from each specimen was measured as relatively wide stipular bracts is a key character for some morphological groups. The more useful width of stipular bracts is shown in Fig. 48C. Of these groups, *M. involucratus* is the most notable, often having very wide stipular bracts that are easily detected. The likely related *M. palmeri* somewhat overlaps in stipular bract width measurements compared to *M. involucratus* but generally has smaller stipular bracts. Outside of *M. palmeri* sensu Bates, wide stipular bracts are less easily detected but distinguish both *M. aboriginum* and *M. enigmaticus* from the rest of the genus. This character is also somewhat prominent in the “Baja East” group that is possibly related to *M. enigmaticus*. The remainder of the genus generally have linear to scale-like stipular bracts with occasional outliers due to fusion of two stipular bracts, which is likely at least partly the cause of wider stipular bracts in those groups where they are prominent. There are distinctions in length of stipular bracts between morphological groups as well (Fig. S9), but these mostly follow the patterns of the calyx bracts, which are much easier to assess.

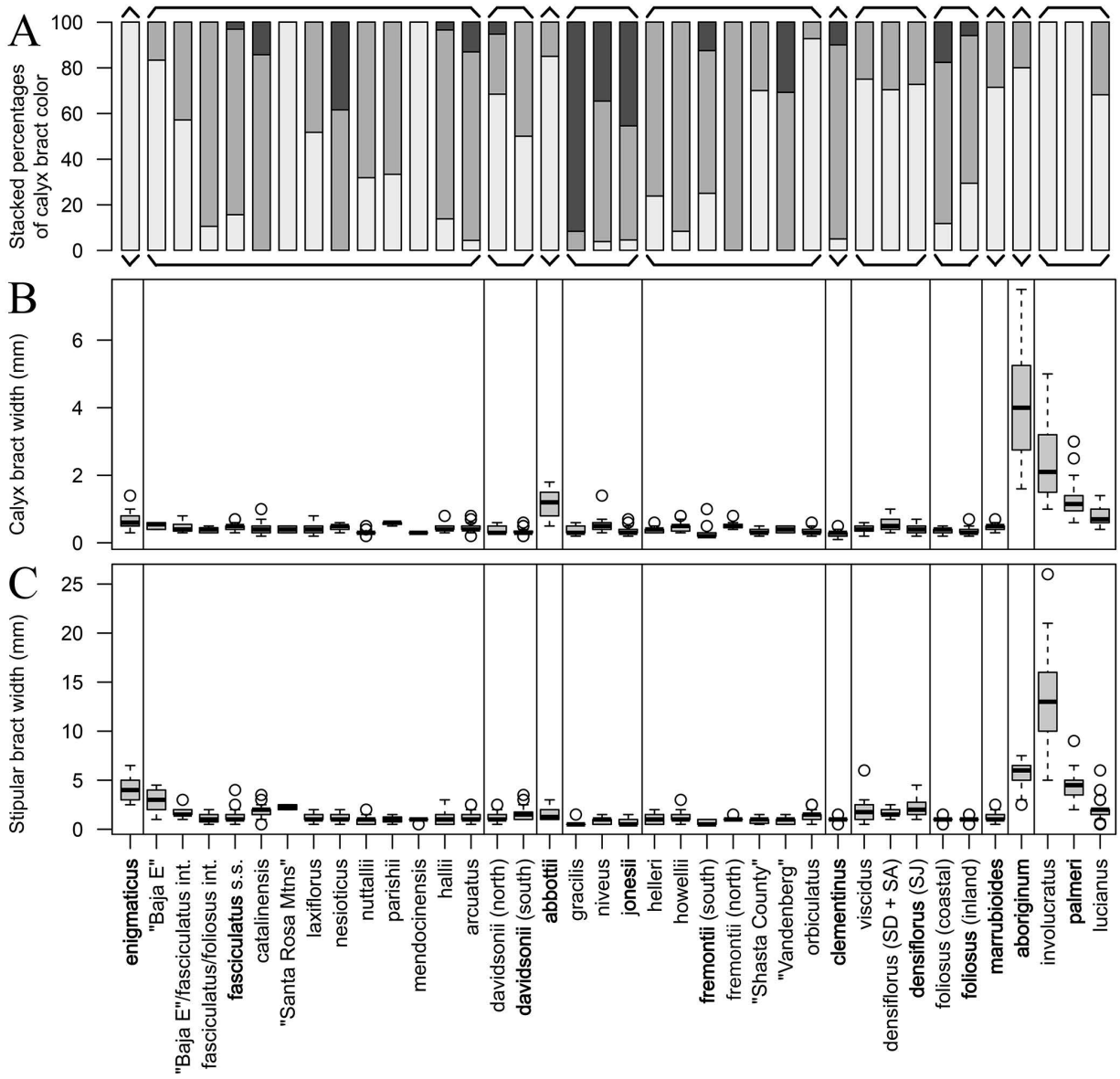

Figure 48. A) Stacked barplots showing the proportion of each calyx bract color category within each morphological grouping. Bract color (plot color): green (pale grey), partially red/black (medium grey), all or mostly red/black (dark grey). B) Boxplots comparing calyx bract width. C) Boxplots comparing stipular bract width. Brackets (A) and vertical lines (B, C) divide morphological groups into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

4.5 Leaf shape

Quantifying leaf size and shape variation was complicated by multiple factors. Leaf size varies throughout the year in *Malacothamnus* with plants having larger leaves in the winter and spring that are dropped in the summer and replaced by smaller leaves that are presumably more drought tolerant. Observations of plants growing at California Botanic Garden indicate the final size of the leaves sprouting in summer may be related to water availability as some plants of the same taxa that were more regularly watered had larger leaves than those that were not. Additionally, the leaves of many specimens were poorly pressed making them impossible to accurately measure without removing them from the specimen and rehydrating. Due to these factors, I did not measure leaf size, though it would be worth investigating, particularly in populations of live plants where the full plant can be considered to assess the full variation. Leaf shape in *Malacothamnus* can also be highly variable. Bates (1963) noted that in one population he examined of *M. fasciculatus* that "practically every leaf shape in the genus is duplicated". Despite this, both degree of leaf lobing and the shape of the leaf base have been used to distinguish taxa. Again, quantifying these was made problematic by many poorly pressed specimens.

To assess the utility of leaf shape in distinguishing taxa and whether leaf shape is worth exploring further, I used four very simplistic categorical measures. Leaf lobing was assessed as not lobed, slightly lobed, or obviously lobed (Fig. 49A). Every morphological group had some specimens with slight leaf lobing, which makes only the extreme categories useful. Three varieties of *M. fasciculatus* (*catalinensis*, *nesioticus*, and *nuttallii*) had most specimens with obvious leaf lobing, the general trend of which, in combination with other characters, may help in differentiating these varieties from the rest of the species. On the other end of the spectrum, the three species within *M. jonesii* sensu Bates are the only groups to have over 50% of specimens with no lobing.

As I had previously noticed multiple leaf base shapes on a single stem, I assessed leaf base shape with presence or absence of three categories: cordate (including subcordate), truncate, and cuneate (including subcuneate). These are shown as the percent of specimens having each leaf base type (Fig. 49 B-D). No clear taxon boundaries could be defined using just leaf base shape, but there are general patterns that may be useful. For example, within *M. fremontii* sensu Bates, *M. helleri* is the only morphological group to commonly have cuneate leaf bases whereas the rest tend towards more cordate leaf bases. Overall, while only somewhat useful due to a high degree of overlap between and within groups, these categorical assessments of leaf shape do indicate that a more quantitative approach or finer-scale and better-defined categories would likely be at least somewhat useful in delineating morphological groups.

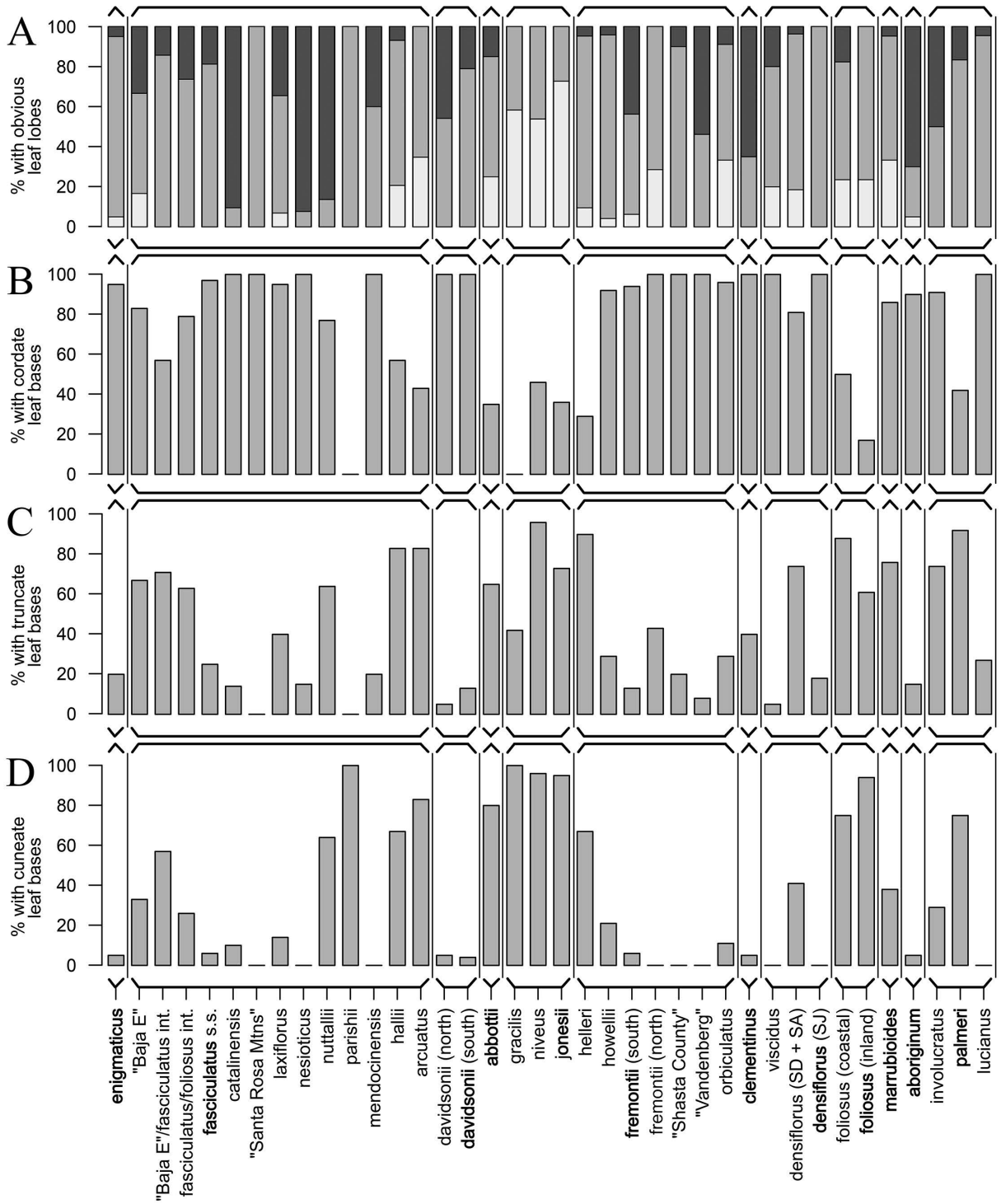

Figure 49. A) Stacked barplots showing the proportion of each leaf lobing category within each morphological grouping: not lobed (pale grey), slightly lobed (medium grey), obviously lobed (dark grey). B–D) Barplots showing percent of specimens in each morphological group with the following: (B) Leaf base cordate to subcordate. (C) Leaf base truncate. (D) Leaf base subcuneate to cuneate. Vertical lines and brackets divide morphological groups into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

4.6 Trichomes

Stellate trichome rays were measured from both the center of the abaxial side of the calyx and from the center of the stem internode below the inflorescence. The mean of a single ray measured from 10 adjacent trichomes was used to approximate the mean ray length for each of these surfaces. As this sample size and sample area often did not account for the full variation seen on these surfaces, I additionally searched for and measured the shortest and longest rays beyond the center of each area to better represent the variation. These were occasionally outliers but often accounted for sparser trichomes of different sizes not represented in the small sample used to approximate the mean. For example, a stem may be densely covered in short trichomes that are accounted for in the main sample and sparsely covered in long trichomes that are only accounted for by the measure of longer rays outside the main sample area. One finding of note is that the length of trichome rays, even on a single stellate trichome, is often highly variable. Related to this, the shortest rays measured were found not to be of practical use as rays of the shortest length recorded (0.1 mm) were found in all morphological groups, though less common in some (Figs. S10 and S11). The mean and the longest rays on both the calyx and stem were useful in distinguishing morphological groups (Fig. 50). A good example of the utility of stellate trichome ray length is in *M. densiflorus* sensu Bates. *Malacothamnus densiflorus* var. *viscidus* (viscidus in the boxplots) has a much shorter mean ray length on the calyx than the rest of *M. densiflorus*, however, the longest stem rays are much longer in *M. d.* var. *viscidus* even though the mean length on the stem is similar. A very useful field character for distinguishing some morphological groups is how discernable the trichome rays are without magnification (Fig. 51). Stellate trichome rays 0.1–0.2 mm cannot be distinguished without magnification, though the color and texture of a surface covered in such short trichomes may suggest it is covered by something. Rays ~0.5 mm and greater are long enough for a surface to appear clearly pubescent without magnification.

Also of note is that the number of rays on stellate trichomes can vary by taxon. This study didn't go into much detail there but did examine whether or not the abaxial surface of a calyx had simple or bifurcate nonglandular trichomes, presumably a reduced form of the stellate trichomes with more rays (Fig. S12). These were only commonly found on the abaxial calyx surface in the two regional groups of *M. densiflorus* var. *densiflorus*. They were also found on three specimens of *M. d.* var. *viscidus* and, examining additional specimens outside those measured for this study, on a single specimen of *M. lucianus*. Simple nonglandular trichomes were, however, commonly observed in other morphological groups on the adaxial calyx surface, which was not evaluated in this study. Slotta (2004) assessed the number of rays on stellate trichomes and found a wide range in the numbers in all taxa that mostly overlap between taxa. Outside of the simple to bifurcate trichomes assessed in my study, Slotta's study suggests that there may be patterns in the maximum number of rays on stellate trichomes with many taxa topping out at 30+ rays and others with the highest around 20. Outside of the long, sparse, and few-rayed stellate trichomes on the calyx of *M. densiflorus* var. *densiflorus*, which are relatively easy to assess, there is, however, likely little practical utility in using number of stellate trichome rays to distinguish between morphological groups.

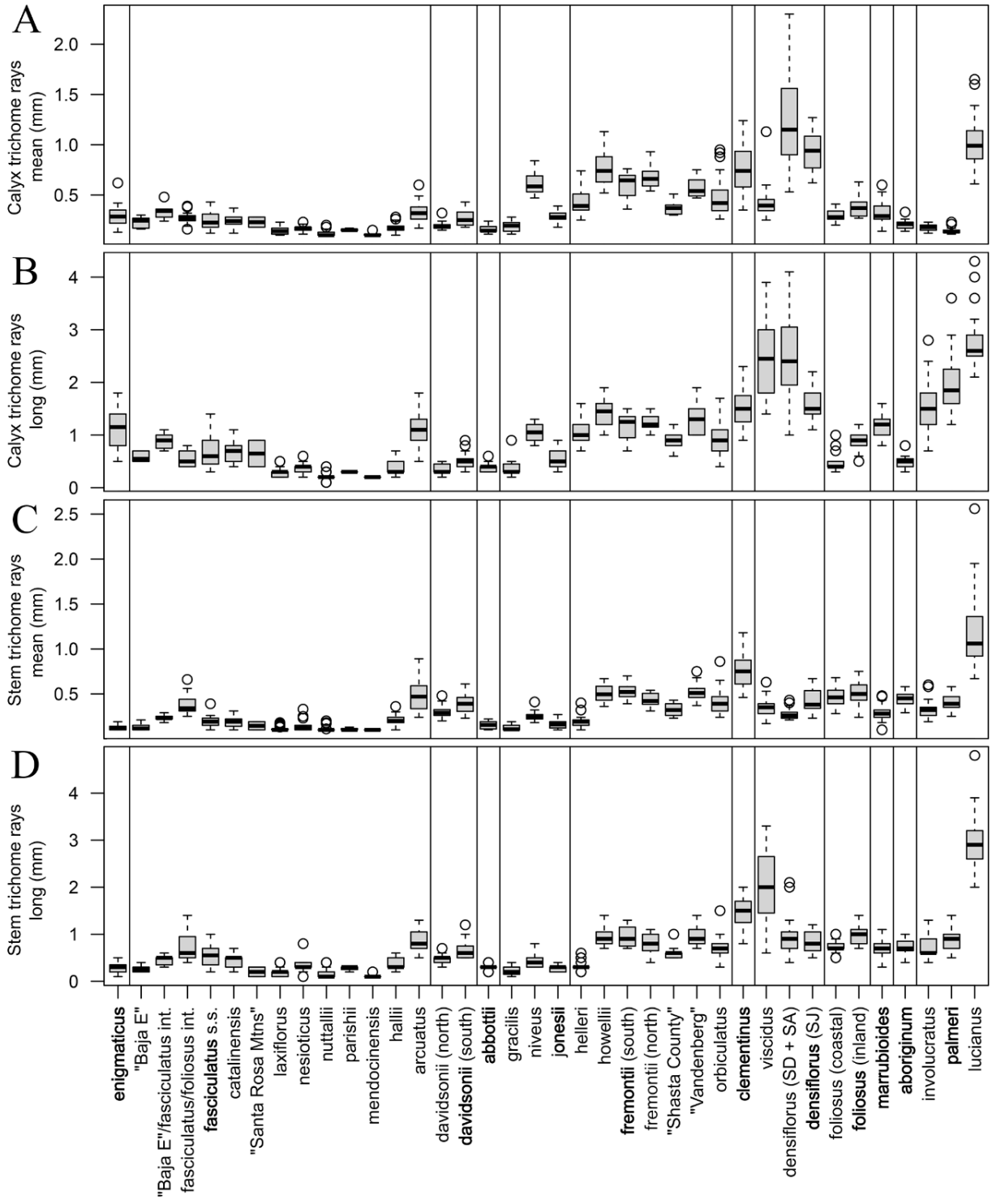

Figure 50. Boxplots comparing stellate trichome ray length of morphological groupings. A. Mean on calyx. B. Longest on calyx. C. Mean on stem. D. Longest on stem. Vertical lines divide morphological groups into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

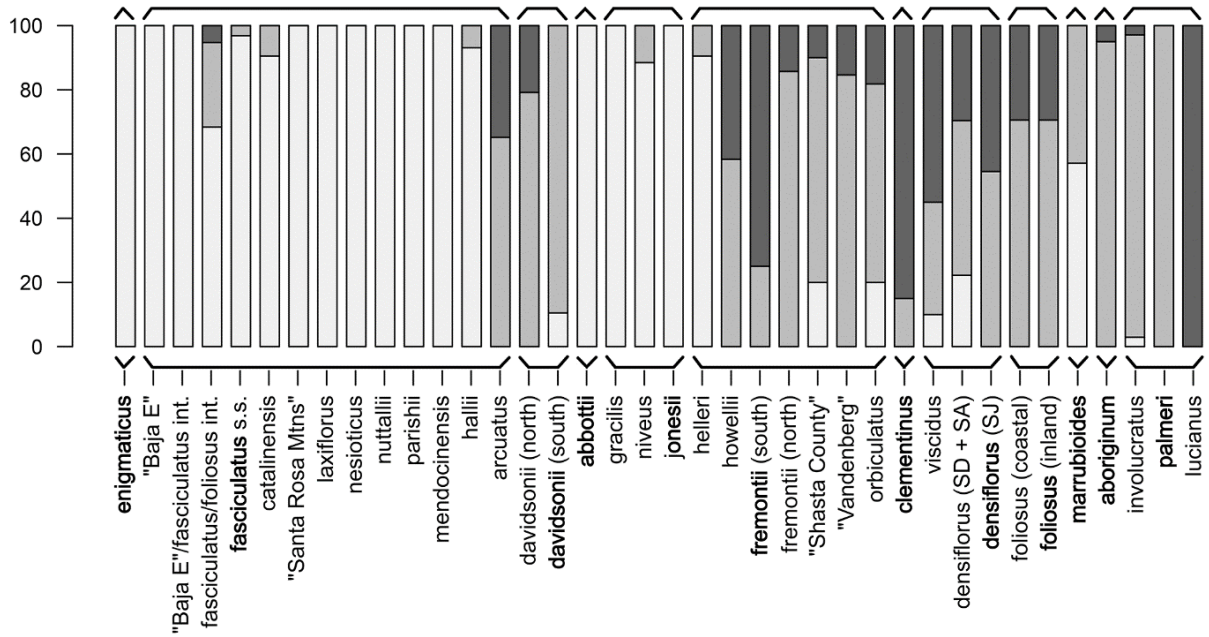

Figure 51. Stacked barplots showing the proportion of specimens with stem stellate trichome rays discernable without magnification within final morphological groupings. Rays discernable: no (pale grey), slightly (medium grey), clearly (dark grey). Brackets divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

The same measurements taken on stellate trichome rays were also taken on glandular trichomes. Exploration with scanning electron microscopy indicates that simple glandular trichomes are likely present in all morphological groups of *Malacothamnus*, however, they are too small to measure under a dissection microscope for some groups. To keep measurements practical, all glandular trichomes less than 0.1 mm long were recorded as 0 mm. Relatively large glandular trichomes were found very useful in delineating morphological groups (Fig. 52). In the majority of morphological groups, glandular trichomes are not readily apparent. Even in those groups with longer glandular trichomes, they can be somewhat difficult to detect at times. In a few morphological groups they are especially prominent though. Longer glandular trichomes clearly separate *M. gracilis* from the rest of *M. jonesii* sensu Bates, the Vandenberg plants from the rest of *M. fremontii* sensu Bates, *M. densiflorus* var. *viscidus* from the rest of *M. densiflorus* sensu Bates, and *M. lucianus* from the rest of *M. palmeri* sensu Bates. Longer glandular trichomes are seen on the calyx of many groups but are also notably longer on the stem in the Vandenberg plants, *M. densiflorus* var. *viscidus*, and *M. lucianus*. While generally clear to slightly yellow in color, it is interesting to note that the glandular trichomes in *M. gracilis* are often reddish, which is apparent in bud even without magnification. Also, in *M. densiflorus* var. *viscidus* and occasionally in the Vandenberg plants the glandular trichomes sometimes dry with a bright green color that may persist on some specimens for 100+ years. Plants with longer glandular trichomes may also have a somewhat rancid odor. This is especially common in *M.*

lucianus and *M*. *densiflorus* var. *viscidus*. While the shortest glandular trichomes measured (Figs. S13 and S14) are more useful than the shortest stellate trichome rays, there is more utility in the easier to assess longer trichomes and the mean.

Leaf trichome density was measured as the mean of 10 distances between the centers of stellate trichomes on both the adaxial and abaxial side of leaves. These characters are most useful in distinguishing morphological groups within *M. fasciculatus* sensu Bates and *M. palmeri* sensu Bates where certain groups have much sparser stellate trichomes on the adaxial leaf surface relative to the abaxial (Fig. 53) and/or may be denser or sparser relative to other morphological groups on a single surface (Fig. 22). *Malacothamnus involucratus* represents the extreme in ratio of stellate trichomes on the adaxial to abaxial leaf surface, with trichomes generally being very sparse to occasionally glabrous on the adaxial leaf surface and much denser on the abaxial surface. *Malacothamnus fasciculatus* var. *nuttallii* offers the other extreme, generally having both a high density of trichomes on the adaxial leaf surface and having similar trichome densities on both the adaxial and abaxial surfaces. Figure 54 shows stellate trichome density separately for each leaf surface.

Additional broad categorical measures of stellate trichome density were also included in this study. While Morse and Chester (2019) found quantitative measures of stellate trichome density on the stem to be very useful in distinguishing species, their assessment of this character was very time-consuming and impractical for use in diagnostic keys. Attempting a simpler measure for use in keys, I assessed whether the surface of the calyx or stem could be seen though the trichomes without magnification with categories being no, slightly, or clearly. This was assessed on the calyx lobes (Fig. 55A), calyx tube (Fig. 55B), on the stem near the base of the inflorescence (Fig. 55C), and on the stem distally in the inflorescence (Fig. 55D). These measures are most useful in distinguishing *M. densiflorus* s.l. and *M. lucianus* from the rest of the genus as each often have very sparse stellate trichomes relative to other taxa. The utility doesn't extend much beyond that though due to the oversimplicity of the categories. The one strong exception is for the density of the trichomes on the calyx tube in *M. densiflorus* (Fig. 55B), which is a useful character in distinguishing the varieties. One confounding factor in using broad categories for trichome density is the length of stellate trichome rays. Sparser trichomes with longer rays may obscure the surface as much as very dense trichomes with very short rays. Therefore, broad categories of stellate trichome density are most useful in combination with trichome ray length. Also notable is that stellate trichome density on the stem was sparser distally in the inflorescence of many morphological groups, which should be considered if assessed further or used in keys.

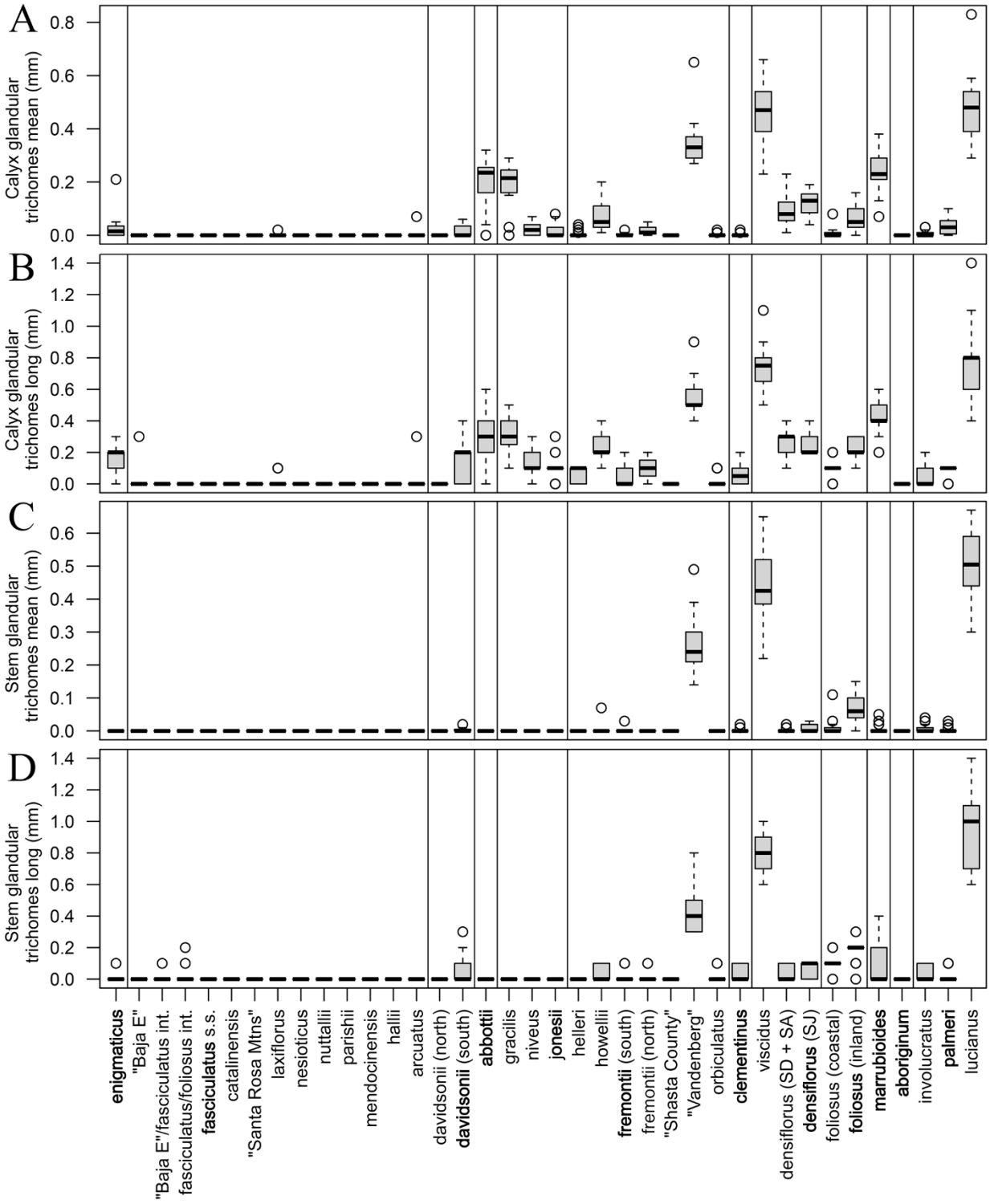

Figure 52. Boxplots comparing glandular trichome length of morphological groupings. A. Mean on calyx. B. Longest on calyx. C. Mean on stem. D. Longest on stem. Vertical lines divide morphological groups into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

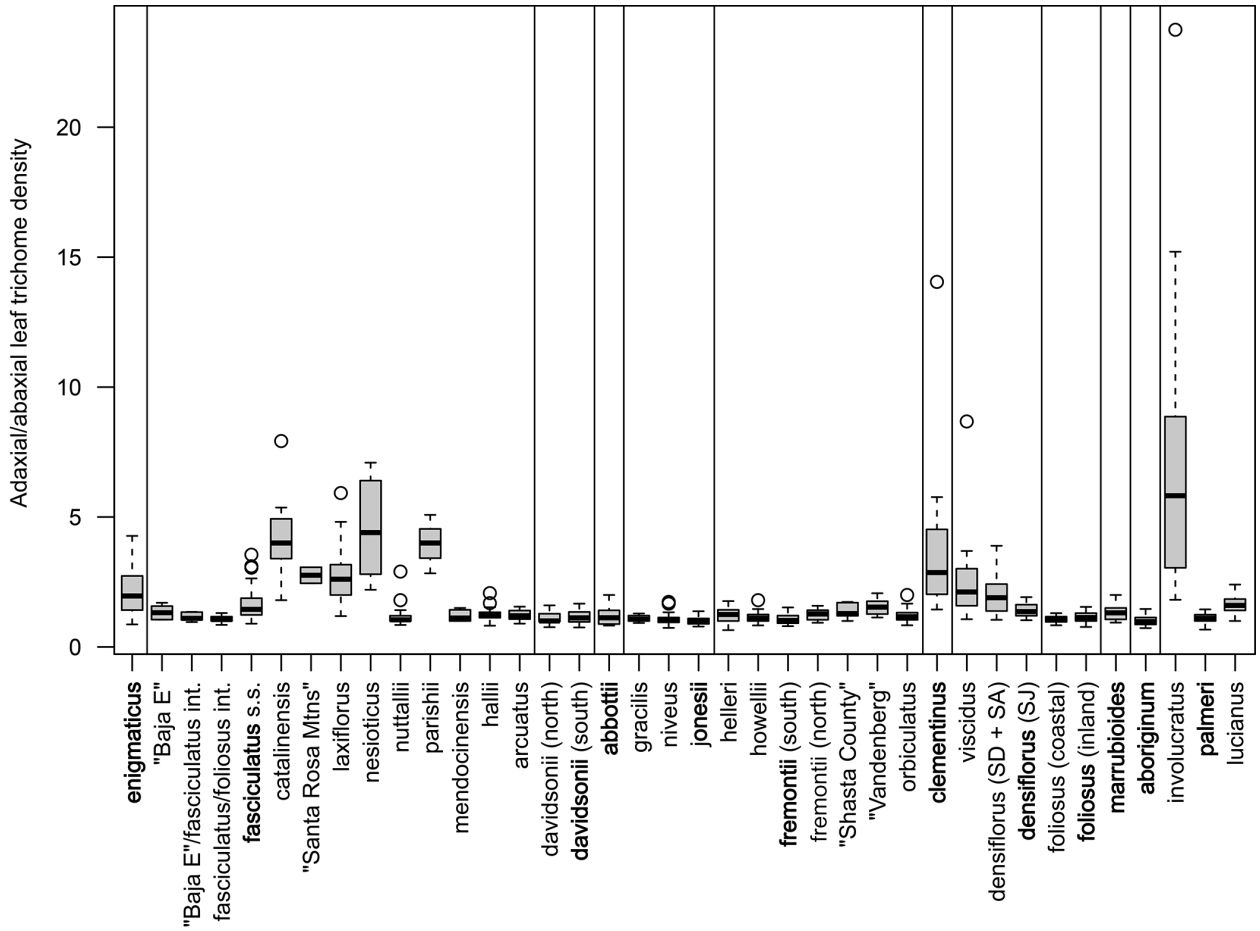

Figure 53. Boxplots showing ratio of adaxial to abaxial leaf stellate trichomes density for final morphological groupings. Higher numbers indicate trichomes are sparser on the adaxial side of the leaf. Note the five specimens with sparsest adaxial trichomes in *M. involucratus* were removed from this data set to better visualize the other groups. Excluding one specimen that is adaxially glabrous, *M. involucratus* tops out at an adaxial/abaxial ratio of 51:1. Vertical lines divide morphological groups into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

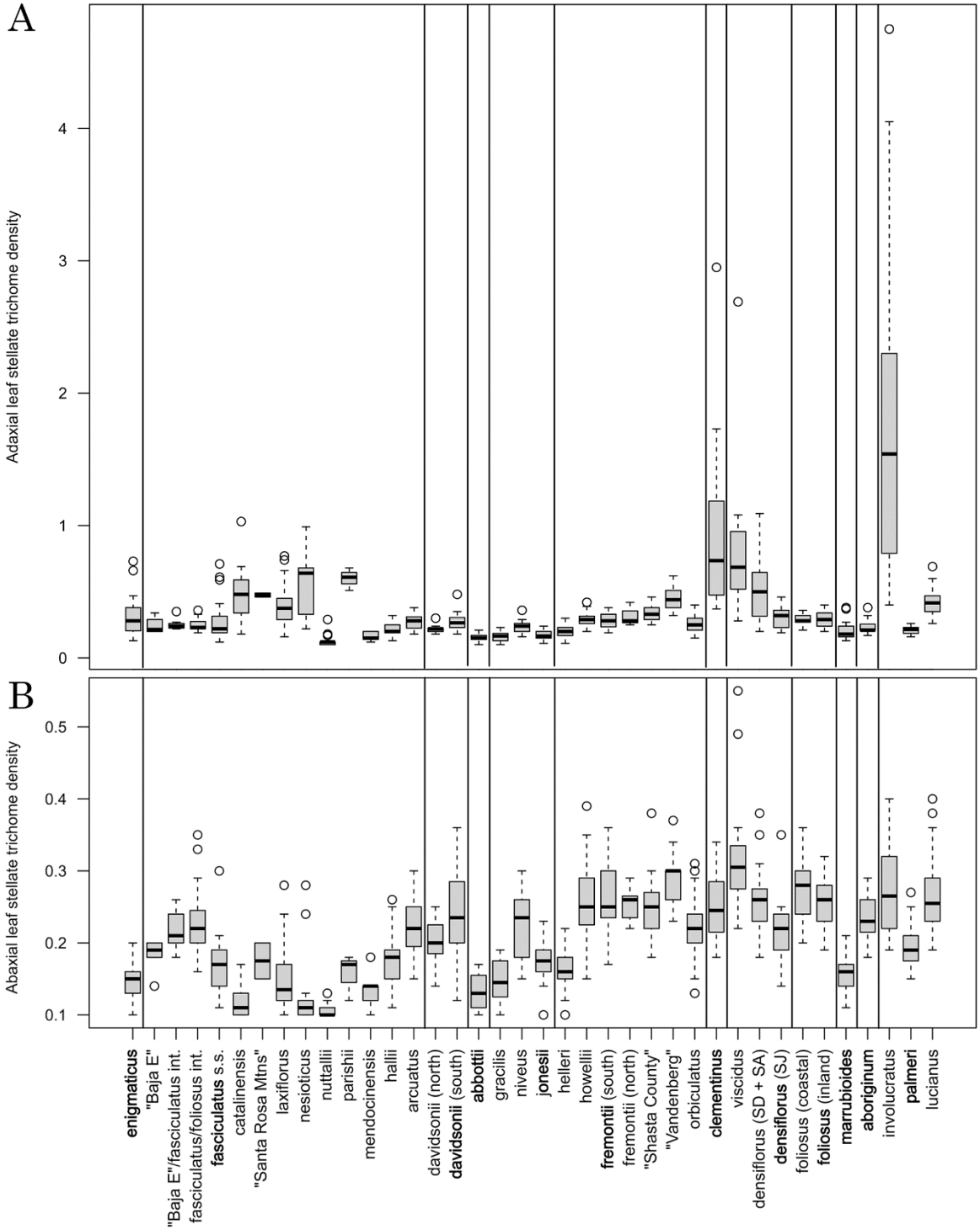

Figure 54. Boxplots showing mean distance in mm between centers of stellate trichomes on adaxial (A) and abaxial (B) leaf surfaces for final morphological groups. Higher numbers indicate trichomes are sparser. Note the five specimens with sparsest adaxial trichomes in *M. involucratus* were removed from this data set to better visualize the other groups. One specimen of *M. involucratus* was adaxially glabrous. Vertical lines divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

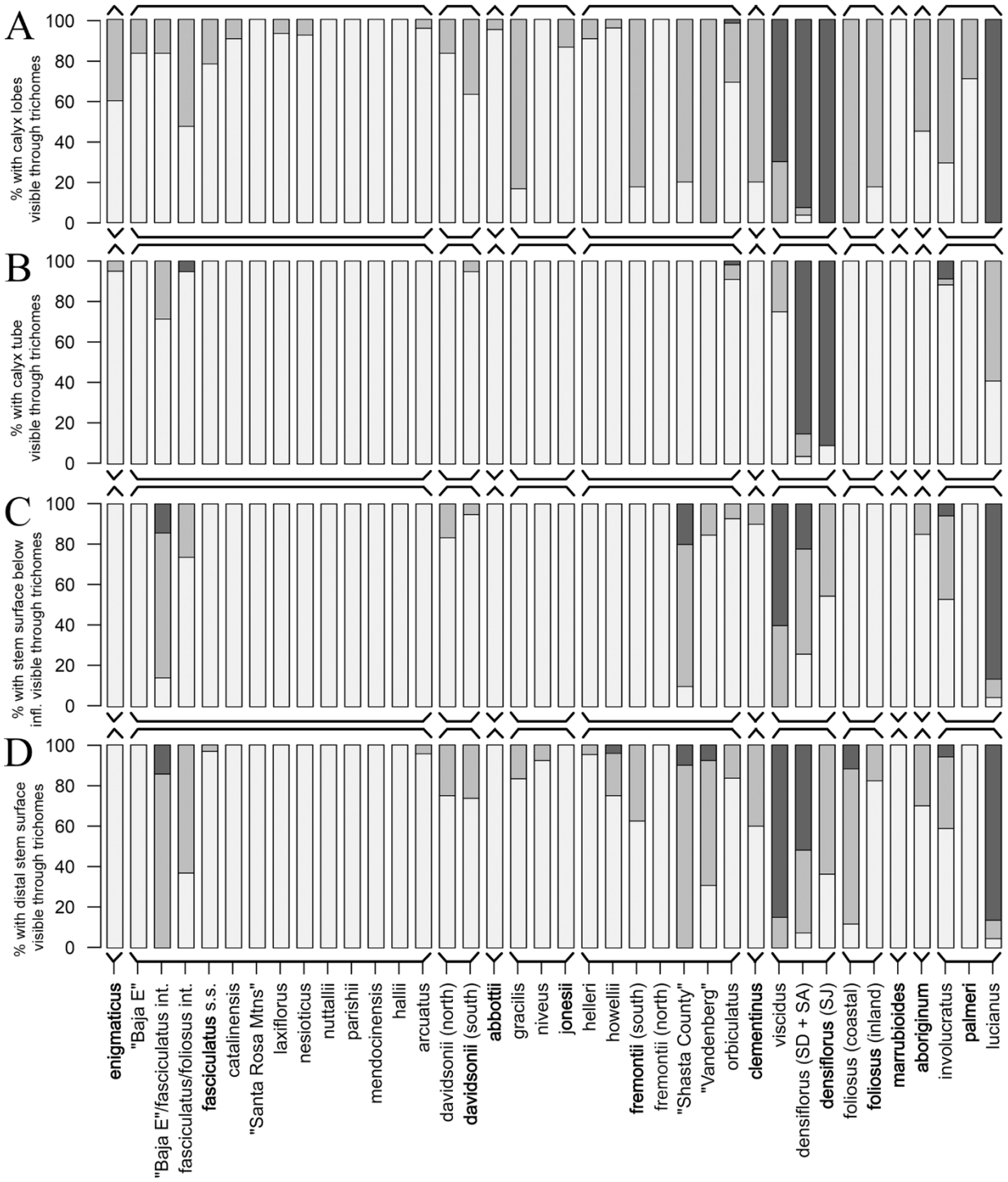

Figure 55. Stacked barplots showing the proportion of specimens with the calyx or stem surface visible through stellate trichomes without magnification within the final morphological groupings. A) calyx lobes, B) calyx tube, C) stem below inflorescence, D) stem in distal part of inflorescence. Surface visible: no (pale grey), slightly (medium grey), clearly (dark grey). Brackets divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

5 CONCLUSIONS

While the 11 *Malacothamnus* species as recognized by Bates are generally reasonable hypotheses of broad taxon groupings based on greatest morphological similarity, the analyses in this study indicate all 28 taxa recognized by Kearney are reasonable taxon hypotheses to assess phylogenetically (taxonomic comparison in Fig. 1). Including the recently described *M. enigmaticus*, 10 additional morphological groups are deemed reasonable hypotheses of taxa to possibly recognize. The 38 morphological groups proposed in this study range from clear species that are geographically isolated and morphologically distinct to intergrading forms needing further evidence to base taxonomic decisions upon (Table 19). All 38 groups follow geographic patterns where most are geographically disjunct from or adjacent to others. See Fig. 44 for relative morphological similarity between these groups.

Table 19. List of the 38 morphological groups recovered in this study. Asterisks denote groups that do not include a type specimen and need further evidence to clarify whether they should be described as new taxa or not. The choice of groups the type specimens were assigned to for *M. paniculatus* (within *M. foliosus*) and *M. fremontii* s.s. are debatable and may need further assessment if recognizing the undescribed groups within them is warranted. What is generally defined as *M. paniculatus* is called *M. foliosus* (coastal) here but excludes the type of *M. paniculatus*, which was placed in *M. foliosus* (inland). Two regions of *M. densiflorus* are abbreviated below. SJ = San Jacinto Mountains. SD + SA = San Diego County region + Santa Ana Mountains.

M. abbottii	*M. fremontii* (south)
M. aboriginum	*M. gracilis*
M. arcuatus	*M. hallii*
M. clementinus	*M. helleri*
M. davidsonii (north)*	*M. howellii*
M. davidsonii (south)	*M. involucratus*
M. densiflorus var. *densiflorus* (SD + SA)*	*M. jonesii*
M. densiflorus var. *densiflorus* (SJ)	*M. lucianus*
M. densiflorus var. *viscidus*	*M. marrubioides*
M. enigmaticus	*M. mendocinensis*
M. fasciculatus var. *catalinensis*	*M. niveus*
M. fasciculatus var. *fasciculatus*	*M. orbiculatus*
M. fasciculatus var. *laxiflorus*	*M. palmeri*
M. fasciculatus var. *nesioticus*	*M. parishii*
M. fasciculatus var. *nuttallii*	"Baja East"*
M. fasciculatus/*foliosus* intermediates*	"Baja East"/fasciculatus intermediates*
M. foliosus (coastal)*	"Santa Rosa Mountains"*
M. foliosus (inland)	“Shasta”*
M. fremontii (north)*	“Vandenberg”*

While some of the taxa recognized by Kearney are clearly morphologically distinct, several are less so. Questionable morphological boundaries lie between *M. fremontii* s.s. and *M. howellii*, *M. foliosus* and *M. paniculatus*, and the varieties of *M. fasciculatus*.

Of those, *M. paniculatus* is possibly taxonomically problematic as the type specimen may be intermediate between coastal forms of *M. foliosus* sensu Bates, which are generally associated with *M. paniculatus,* and more inland forms, which are generally associated with *M. foliosus* s.s. What has been historically considered *M. paniculatus* (possibly excluding the type), I call the *M. foliosus* (coastal) group.

Despite some morphological ambiguity between the varieties of *M. fasciculatus*, three of these varieties are geographically isolated, possibly leaving only the boundary of the geographically adjacent *M. f.* var*. fasciculatus* and *M. f.* var. *laxiflorus* problematic.

Some other geographically adjacent species appear mostly distinct but intergrade. These are *M. arcuatus* with *M. hallii* and *M. niveus* with both *M. gracilis* and *M. jonesii*.

Malacothamnus densiflorus var. *viscidus* was found to be distinct from the rest of *M. densiflorus* sensu Bates, however, all previous treatments included many plants that did not fit well with plants from the type locality of *M. d.* var. *viscidus*. This paper redefines the diagnostic morphological characters distinguishing *M. d.* var. *viscidus* from rest of *M. densiflorus*, removing previous ambiguities between the two varieties (see Chapter 3.4).

One species that is presumed extinct, *M. parishii*, is represented by only three specimens from the type collection (Parish 3804) collected in 1895 and possibly two additional specimens (Parish 7136) from 1909. PCA indicates these are possibly distinct from or an extreme form of the geographically adjacent *M. fasciculatus* var. *laxiflorus*. Phylogenetic evidence is likely needed to confirm the relationship of *M. parishii* to *M. fasciculatus* var. *laxiflorus*, though the age of the *M. parishii* specimens may prove problematic for sequencing and the highly urbanized type locality means newer specimens are unlikely to be collected.

Another possibly problematic taxon, which also lacks relatively recent specimens to assess phylogenetically, is *Malvastrum thurberi*. The type locality of *Malvastrum thurberi* is geographically disjunct from the rest of the genus, collected in Arizona or adjacent Mexico, and has only been collected in that area once in 1852. PCAs place it within the morphological variation of *Malacothamnus fasciculatus* s.s., which follows the pattern of the disjunct *M. orbiculatus* in Arizona. This implies that, in the past, both *M. fasciculatus* s.s. and *M. orbiculatus* may have been more widespread to the east of where their core ranges now occur. As *Malvastrum thurberi* is not morphologically distinguishable from *M. fasciculatus* s.s. in these analyses, I include it in *M. fasciculatus* s.s. However, if new plants are ever found near the type locality, *Malvastrum thurberi* should be reassessed.

Nine morphological groupings were found in PCAs that may be morphological variants within currently described taxa, intermediates due to hybridization, or undescribed taxa. “Shasta” and “Vandenberg” are clearly both geographically and morphologically distinct from similar taxa. The remaining groupings are less clear. The “Baja East” group may be an undescribed taxon related to *M. enigmaticus*. Two possible hybrid groups in Baja California may be intermediates of *M. fasciculatus* s.s with both *M. foliosus* sensu Bates and the “Baja East”

group. A small group of specimens from the Santa Rosa Mountains most closely fits the morphology of *M. fasciculatus* var*. laxiflorus* but may be intermediate with the nearby *M. densiflorus* and/or *M. enigmaticus*. *Malacothamnus davidsonii* occurs in two disjunct regions with plants from these regions being somewhat morphologically divergent based on PCA, though it would be difficult to accurately identify the source region of many specimens based on morphology. The geographic gap between the two *M. davidsonii* regions indicates at least a recent lack of gene flow between them, which indicates they could possibly be morphologically cryptic taxa. Specimens from near the type locality of *M. densiflorus* in the San Jacinto Mountains appear to be somewhat morphologically divergent from the rest of *M. densiflorus* var. *densiflorus*, which again indicates possible cryptic taxa. *Malacothamnus howellii*, as provisionally delineated in this study, geographically separates *M. fremontii* s.s. into disjunct northern and southern regions. Whether *M. fremontii* s.s. should be split into two geographic groups and what the relationship of *M. howellii* is to these groups is not clear based on morphology.

This morphological assessment of taxon hypotheses of previous *Malacothamnus* researchers serves as an example that improved sampling of both characters and specimens can help validate and/or clarify taxon boundaries in problematic taxonomic groups even when multiple previous morphological analyses have been much less successful. This is especially important to consider when taxa of conservation concern are involved. Bates (1993) reduced the 28 *Malacothamnus* taxa of Kearney (1951, 1955) to only 11 taxa. Ten of the taxa Bates reduced to synonymy with other taxa are considered of conservation concern in California (CNPS 2022). Evidence from the morphological analyses of this study revealed not only two clearly distinct undescribed morphological groups in *Malacothamnus* but that all of the taxa recognized by Kearney and seven other undescribed morphological groupings have at least some level of morphological support for recognition. While many of these taxa are both morphologically and geographically distinct, this study also identifies more ambiguous groupings that are perhaps best recognized as varieties, hybrids, or only as variation within a single taxon. Taxonomic decisions regarding more ambiguous groupings should ideally rely on multiple lines of evidence. To support this, the morphological groupings from this study are tested phylogenetically as hypothesized lineages in Volume 2 of this monograph and a new treatment of the genus is presented in Volume 3.

Data Repository

Data available from Figshare: https://doi.org/10.6084/m9.figshare.23936862

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Appendix 1 - Specimens Measured

Herbarium voucher specimens of *Malacothamnus* used in this study are listed alphabetically by taxon followed by unnamed morphological groups. Within each they are organized by location to the county level, then alphanumerically by collector and collection number. When multiple morphological groups are represented under a single taxon, the morphological group name is underlined and specimens in that group follow. Sample size for each morphological group is noted with "n =". Type specimens are bolded and, if a synonym, labeled with the basionym. An asterisk notes 2+ specimens were measured from a single voucher sheet or duplicates of currently unaccessioned specimens. A tilde denotes specimens grown from seed at California Botanic Garden that are listed by the county of the seed origin. Specimens not yet accessioned are marked with accession number as TBD (to be determined). At least one sheet of each TBD collection will be housed at RSA.

Malacothamnus abbottii (Eastw.) Kearney (n = 20). USA. California: Monterey County: *E. K. Abbott s.n. 9 Jan 1889* (**CAS52708 - Holotype**), *M. A. Elvin & V. Yadon 332* (RSA785791), *M. A. Elvin & V. Yadon 333* (RSA785793), *M. A. Elvin & V. Yadon 334* (RSA785790), *M. A. Elvin & V. Yadon 337* (RSA785794), *M. A. Elvin & V. Yadon 338* (RSA785795), *M. A. Elvin & V. Yadon 339* (RSA786442), *M. A. Elvin & V. Yadon 340* (RSA786441), *M. A. Elvin & V. Yadon 341* (RSA786440), *M. A. Elvin & V. Yadon 343* (RSA786439), *M. A. Elvin & V. Yadon 345* (RSA786438), *K. Morse M268a* (TBD*), *K. Morse M270* (TBD*), *K. Morse M271* (TBD*), *K. Morse M397* (TBD), *V. Yadon s.n. 7 Jun 1990* (RSA518393), *V. Yadon s.n. 17 Aug 1996* (RSA645646).

Malacothamnus aboriginum (B.L. Rob.) Greene (n = 20). USA. California: Fresno County: *M. Denslow et al 1101* (RSA681318), *R. S. Ferris & R. C. Bacigalupi s.n. 28 May 1941* (RSA27099), *L. P. Janeway 1783* (DAV106253), *K. Morse M240* (TBD*), *L. S. Rose s.n. 11 May 1936* (RSA15510). Monterey County: *K. Morse M180* (TBD). San Benito County: *M. K. Curran s.n. 6 Jan 1885* (**CAS741 - Holotype**), *M. A. Elvin & V. Yadon 329* (RSA785788), *F. R. Fosberg 54995* (RSA434858), *C. B. Hardham 12614* (RSA185316), *K. Morse M110* (TBD*), K. Morse M177* (TBD), *K. Morse M178* (TBD), *K. Morse M179* (TBD), *K. Morse M381* (TBD*), *D. W. Taylor et al 21517* (RSA844989), *E. C. Twisselmann 2457* (RSA115500*), C. B. Wolf s.n. 25 Sep 1927* (RSA11107).

Malacothamnus arcuatus (B.L. Rob.) Greene (n = 23). USA. California: Alameda County*: J. T. Howell 12579* (CAS221806). San Mateo County: *A. Eastwood 346* (CAS52638), *A. Eastwood & J. T. Howell 7435* (CAS270021), *A. A. Heller s.n. 13 Jul 1901* (CAS186292), *J. W. Howe 186* (HSC16067*), K. Morse & S. Simono M175* (TBD*), *G. Oberlander 258* (DS749625), *J. H. Thomas 9906* (RSA176727). Santa Clara County: *L. R. Abrams 4245* (DS63049), *L. R. Abrams 1019* (DS143275), *W. S. Atkinson s.n. 12 May 1900* (DS606133), *E. Bond s.n. 15 Jun 1928* (POM175447), *E. Cannon s.n. Jun 1899* (CAS52633), *W. R. Dudley s.n. 21 Mar 1898* (DS63048), *W. R. Dudley s.n. 18 May 1895* (DS31513), *A. D. E. Elmer 4802* (DS68669), *V. F. Hesse 971* (DS344290), *K. Morse M174* (TBD), *R. L. Pendleton 1494* (POM89620), *C. B. Wolf 3746* (DS281700). Santa Cruz County: *L. R. Abrams 6383* (DS73765), *A. Eastwood s.n. 30 Sep 1916* (CAS52637).

Malacothamnus clementinus (Munz & I.M. Johnst.) Kearney (n = 20). USA. California: Los Angeles County: *F. C. Boutin 1653* (RSA320826), *F. C. Boutin 1654* (RSA320825), *F. C. Boutin 1655* (RSA320824), *S. Boyd et al 4142* (RSA526148), *S. Boyd et al 4279* (RSA526571), *M. A. Elvin et al 169* (RSA678461), *M. A. Elvin et al 326* (RSA785789), *M. A. Elvin & G. Allan 17* (RSA582910), *S. A. Junak SCI-407* (RSA879009*), *A. Liston et al 76 -1* (RSA515088), *B. Munson BM1* (TBD), *B. Munson BM2* (TBD), *B. Munson BM3* (TBD), *B. Munson BM4* (TBD), *B. Munson BM5* (TBD), *B. Munson BM6* (TBD), *P. A. Munz 6684* (**POM20491 - Holotype***), F. W. Peirson 3458* (RSA77203), *P. H. Raven 17977* (RSA158336).

Malacothamnus davidsonii (B.L. Rob.) Greene. *M. davidsonii* (north) (n = 19). USA. California: Monterey County: *M. A. Elvin & V. Yadon 335* (RSA785792), *C. B. Hardham 10353* (RSA150730), *C. B. Hardham 10358* (RSA150692, RSA150988), *C. B. Hardham 10476* (RSA160011), *K. Morse M268b* (TBD*), *K. Morse M269* (TBD*), *K. Morse M272* (TBD*), *B. Oliver s.n. 28 Sep 1976* (CDA35731), *E. Painter & E. Neese HL- 2236* (RSA799759), *A. Simontacchi 679* (UC1122032), *V. Yadon s.n. 17 Aug 1996* (RSA645647). San Luis Obispo County: *M. A. Elvin & V. Yadon 347* (RSA786589), *C. B. Hardham 2484* (RSA133267), *K. Morse M266* (TBD*). *M. davidsonii* (south) (n = 24). USA. California: Los Angeles County: *A. Davidson s.n. 24 Jun 1895* (**GH00052893 - Lectotype**), *A. Davidson 15855* (RSA350715), *A. Edwards 129* (RSA753963), *A. Edwards 134* (RSA753962), *F. Grinnell Jr. s.n. 19 Aug 1917* (POM21363), *C. Hohn 6* (RSA716604), *K. McDonald & L. Flory s.n. 4 Sep 2002* (RSA699606), *O. Mistretta 814* (RSA643395), *K. Morse M118* (TBD), *K. Morse M258* (TBD*), *K. Morse M315* (TBD), *G. L. Moxley 698* (RSA433280), *P. A. Munz & Johnson 11138* (POM153291), *F. W. Peirson 8180* (RSA77030), *J. C. Roos 331* (POM263063), *R. G. Swinney 13653* (RSA820947), *R. F. Thorne & C. W. Tilforth 39961* (RSA226929), *A. Warniment & J. Pareti ADW- 2* (RSA712212), *L. C. Wheeler 2053* (RSA433278), *L. C. Wheeler 10107* (RSA866348), *L. C. Wheeler s.n. 20 Aug 1968* (RSA610537), *C. B. Wolf 4076* (RSA6078), *C. B. Wolf s.n. 2 Jul 1931* (RSA3231).

Malacothamnus densiflorus* var. *densiflorus (S. Watson) Greene. *M. d.* var. *densiflorus* - San Jacinto Mtns. Region (n = 11). USA. California: Riverside County: *W. L. Jepson & H. M. Hall 1387* (JEPS26394), *K. Morse M331* (TBD*), *K. Morse M387* (TBD*), *S. B. Parish & W. F. Parish 738* (**GH00052894 - Lectotype**). *M. d.* var. *densiflorus* - San Diego County and Santa Ana Mtns. Regions (n = 27). MEXICO. Baja California*: F. R. Fosberg 975* (POM220313*), P. A. Munz 9506* (POM96415), *F. W. Peirson 5884* (RSA77213). USA. California: Orange County: *K. Morse M386* (TBD). Riverside County: *D. L. Banks & S. D. Boyd 456* (RSA586733), *S. Boyd & O. Mistretta 7006* (RSA561079), *K. Morse M046a* (TBD), *K. Morse M047a* (TBD), *K. Morse M048a* (TBD), *K. Morse M392* (TBD), *K. Morse M393* (TBD), *K. Morse M394* (TBD). San Diego County: *Collector unknown s.n. 11 Nov 1928* (RSA700085), *K. Morse M009* (TBD), *K. Morse M050* (TBD), *K. Morse M051* (TBD), *K. Morse M070a* (TBD), *K. Morse M081B* (TBD), *K. Morse M086* (TBD), *K. Morse M215* (TBD*), *K. Morse M216* (TBD), *K. Morse M333* (TBD), *K. Morse M334* (TBD), *K. Morse M336* (TBD), *P. A. Munz 10356* (POM96202), *C. B. Wolf 2131* (RSA2836).

Malacothamnus densiflorus* var. *viscidus (Abrams) Kearney (n = 20). MEXICO. Baja California: *J. P. Rebman 11843* (SD160852). USA. California: San Diego County: *L. R. Abrams 3528* (**DS60886 - Holotype**), *F. F. Gander 223* (UC797617), *R. Moran 17871* (RSA231200), *K. Morse M049* (TBD), *K. Morse M067a* (TBD), *K. Morse M071a* (TBD), *K. Morse M071b* (TBD), *K. Morse M071c* (TBD), *K. Morse M217* (TBD), *K. Morse M218* (TBD), *K. Morse M332* (TBD*), *J. P. Rebman et al 10999* (RSA704420), *Roberson & Kenyon s.n. 26 May 1969* (CDA35736), *A. C. Sanders 26500* (DAV173707, RSA709385), *H. V. D. Werff 47556* (RSA360125).

Malacothamnus enigmaticus K. Morse & T. Chester (n = 20). USA. California: San Diego County: *T. Chester 2153-1* (TBD), *T. Chester 2154-2* (TBD), *T. Chester 2155* (TBD), *T. Chester 2236-G1* (TBD), *T. Chester 2237-G2* (TBD), *K. Morse M021* (TBD), *K. Morse M024* (TBD), *K. Morse M027* (TBD), *K. Morse M040* (TBD), *K. Morse M041a* (TBD), *K. Morse M060a* (TBD), *K. Morse M061a* (TBD), *K. Morse M062b* (TBD), *K. Morse M064a* (TBD), *K. Morse M065d* (TBD), *K. Morse M065g* (TBD), *K. Morse M066d* (TBD), *K. Morse M081A* (TBD*), *K. Morse M214* (TBD).

Malacothamnus fasciculatus* var. *catalinensis (Eastw.) Kearney (n = 21). USA. California: Los Angeles County: *M. B. Dunkle 1932* (RSA433293), *A. Eastwood 6440* (**CA52692 - Lectotype**), *F. R. Fosberg S5425* (POM243806), *M. Hoefs et al 2397* (RSA595427), *K. Morse M339* (TBD), *K. Morse M340* (TBD), *K. Morse M341* (TBD), *K. Morse M342* (TBD), *K. Morse M343* (TBD*), *K. Morse M344* (TBD), *K. Morse M345* (TBD), *K. Morse M346* (TBD*), *K. Morse M347* (TBD), *K. Morse M348* (TBD), *T. S. Ross 6924* (RSA583082),

R. F. Thorne & P. Everett 34473 (RSA177811), *R. F. Thorne & D. Propst 37646* (RSA199200), *B. Trask 190* (RSA433296), *C. B. Wolf 3575* (RSA3902).

Malacothamnus fasciculatus* var. *fasciculatus (Nutt. ex Torr. & A. Gray) Greene (n = 32). MEXICO. Baja California: *C. F. Harbison 45503* (SD45491), *E. B. Higgins s.n. 21 Jun 1946* (SD181296), *R. Moran 11012* (SD54749), *R. Moran 15244* (SD68041), *J. J. P. Navarro 762* (SD141142), *J. P. Rebman 1204* (SD137107), *J. P. Rebman 5107* (SD144264), *J. P. Rebman 5351* (SD145295), *J. P. Rebman 22972* (SD223020), *J. Riley 320* (SD254037), *A. G. Vestal 6023* (SD21815), *I. L. Wiggins 366* (SD94552), *I. L. Wiggins 11899* (SD47284). MEXICO or USA. Sonora/Arizona Border: *G. Thurber 709* (**GH00052911, GH00052912* - *Malvastrum thurberi* Lectotype and Isolectotype**). USA. California: Orange County: *S. D. White & M. Honer 10400* (RSA702686). San Diego County: *A. Herman M042* (TBD), *K. Morse M014* (TBD), *K. Morse M016* (TBD), *K. Morse M017* (TBD), *K. Morse M030* (TBD), *K. Morse M032* (TBD), *K. Morse M036* (TBD), *K. Morse M219* (TBD), *K. Morse M220* (TBD), *K. Morse M337* (TBD), *T. Nuttall s.n. date unknown* (**NY221803 - Lectotype**), *J. P. Rebman et al 20779* (RSA779371), *J. P. Rebman et al 28528* (RSA821119), *S. D. White 7517* (RSA655222), *C. B. Wolf 2074* (RSA2026).

Malacothamnus fasciculatus* var. *laxiflorus (A. Gray) Kearney (n = 58). USA. California: Los Angeles County: *J. Dittes 1396* (RSA739612), *W. O. Griesel s.n. 6 Jul 1962* (RSA152024), *R. Gustafson 2212* (RSA433329), *K. Morse M129* (TBD), *K. Morse M130* (TBD*), *K. Morse M256* (TBD), *K. Morse M352* (TBD), *P. H. Raven & H. J. Thompson 13752* (RSA126677), *T. S. & A. Ross 5682* (RSA550724), *A. C. Sanders & M. A. Elvin 25132* (RSA695387), *R. G. Swinney 9181* (RSA756153), *A. Williams 24-92* (RSA660894). Orange County: *L. M. Booth 838* (POM201634), *M. & C. Breidenbaugh 79* (RSA647942), *F. W. Peirson 4662* (RSA95321), *F. M. Reed 6534* (POM220268), *A. C. Sanders & F. M. Roberts 35677* (RSA751428), *A. C. Sanders & F. M. Roberts 36064* (RSA750004), *T. Sargent s.n. 17 May 1959* (RSA652284). Riverside County: *Mrs. J. D. (Abrams?) 9217* (POM2944), *D. S. Bell & L. Gross 7768* (RSA853683), *I. M. Johnston 2024* (POM2945), *I. M. Johnston s.n. 30 May 1918* (POM2946), *I. M. Johnston s.n. 8 May 1920* (POM9599), *K. Morse M053* (TBD), *K. Morse M054* (TBD), *K. Morse M057* (TBD), *K. Morse M209* (TBD), *K. Morse M211* (TBD*), *K. Morse M324* (TBD), *K. Morse M338* (TBD), *J. D. Olmsted 3614* (RSA433321), *M. L. Overholtzer 274* (RSA519211), *C. W. Tilforth & W. Wisura 1916* (RSA305668), *S. D. White & J. M.* Wood 12444 (RSA740918). San Bernardino County: *N. S. Fraga et al 2527* (RSA740515), *J. Henrickson 20255* (RSA656961), *I. M. Johnston 2279* (POM8818), *K. Morse M119* (TBD), *K. Morse M120* (TBD), *K. Morse M148* (TBD), *K. Morse M149* (TBD), *K. Morse M250* (TBD*), *K. Morse M297* (TBD*), *K. Morse M418* (TBD), *K. Morse M419* (TBD), *K. Morse & M. Tollett M123* (TBD), *S. B. Parish & W. F. Parish 493* (DS118305), *P. H. Raven & R. K. Beeks 16759* (CAS438735, RSA158254). San Diego County: *K. Morse M063a* (TBD). Ventura County: *L. Gross & L. Washburn 7275* (RSA834067), *K. Morse M321* (TBD), *J. M. Wood 4021* (RSA820977).

Malacothamnus fasciculatus* var. *nesioticus (B.L. Rob.) Kearney (n = 13). USA. California: Santa Barbara County: *T. S. Brandegee s.n. Apr 1888* (**UC168556 - Syntype**), *E.L. Greene s.n. Aug 1886* (**GH00052907 - Lectotype**), *R. Hoffmann s.n. 28 Jun 1930* (POM172099), *S. A. Junak SC- 2761* (RSA589005), *K. McEachern s.n. 23 Jul 2020* (SBBG_unaccessioned*), *C. F. Smith 8671* (RSA534277), *R. F. Thorne et al 52510* (RSA305548), *R. F. Thorne et al 52510* (RSA316428), *R. F. Thorne & C. W. Tilforth 47556* (RSA363973).

Malacothamnus fasciculatus* var. *nuttallii (Abrams) Kearney (n = 22). USA. California: San Luis Obispo County: *K. Morse M405* (TBD). Santa Barbara County: *L. R. Abrams s.n. 25 Jul 1908* (**DS31553 - Isotype, DS60885 - Holotype**), *M. Beyers & G. F. Hrusa 149* (CDA29622), *H. C. Forbes 1358* (SBBG85817), *D. J. Keil 25954* (OBI65548), *K. Morse M124* (TBD), *K. Morse M125* (TBD), *K. Morse M126* (TBD), *K. Morse M263* (TBD), *K. Morse M264* (TBD), *M. A. Piehl 62440* (RSA166026), *C. F. Smith 11091* (RSA443486), *S. Swensen 1006* (RSA557803), *C. B. Wolf 10963* (RSA25651). Ventura County: *K. Morse M260* (TBD*), *K.*

Morse M261 (TBD), *K. Morse M262* (TBD), *H. M. Pollard s.n. 29 Aug 1963* (RSA433327), *H. M. Pollard s.n. 30 Jun 1946* (RSA34855), *S. D. White & D. Ray 13103* (RSA748708).

Malacothamnus foliosus (S. Watson) Kearney. *M. foliosus* (inland) (n = 17). MEXICO. Baja California: *R. F. Hoover 56023* (RSA31026, SD124043), *R. Moran 24258* (SD97339), *K. Morse & J. Riley M355* (TBD*), *K. Morse & J. Riley M356* (TBD*), *C. R. Orcutt 1237* (**UC109091* - Isotype**), *C. R. Orcutt s.n. 14 Jul 1885* (**GH52906 - Lectotype of *M. paniculatus***), *C. R. Orcutt s.n. Sep 1884* (**GH00052896* - Lectotype**), *I. L. Wiggins 11869* (SD47285). *M. foliosus* (coastal) (n = 17). MEXICO. Baja California: *J. Campos Sauzal1* (TBD*), *J. Campos Sauzal2* (TBD), *R. Moran 16025* (RSA206993, SD71522), *R. Moran 16515* (RSA207430, SD71923), *R. Moran 22923* (RSA293886, SD95506), *R. Moran 26120* (SD100579), *R. Moran 29838* (SD109026), *K. Morse & J. Riley M354* (TBD*), *K. Morse & J. Riley M358* (TBD*), *L. S. Rose 58123* (RSA118773).

Malacothamnus fremontii (Torr. ex A.Gray) Greene. *M. fremontii* (north) (n = 7). USA. California: Sutter County: *L. Ahart 2435* (CAS833968), *L. Ahart 2435* (CHSC45941), *L. Ahart 5019* (CAS776956), *H. A. Borthwick 1822* (DAV6161). Tehama County: *B. Castro & L. P. Janeway 972* (CHSC77603), *J. Molter 749b* (CHSC92157). Yuba County: *K. Morse M414* (TBD). *M. fremontii* (south) (n = 16). USA. California: Fresno County: *K. Morse M202* (TBD), *K. Morse M374* (TBD), *K. Morse M375* (TBD*), *K. Morse M376* (TBD). Madera County: B. Crampton 1471 (AHUC19942), J. Street s.n. 25 Jul 1950 (AHUC18818). Tulare County: *K. Morse M103* (TBD), *K. Morse M203* (TBD), *K. Morse M204* (TBD*), *K. Morse M372* (TBD), *K. Morse M373* (TBD). County Unknown: *J. C. Fremont s.n. 1946* (**GH00052927 - Isolectotype**).

Malacothamnus gracilis (Eastw.) Kearney (n = 12). USA. California: San Luis Obispo County: *A. Eastwood 14996* (**POM224487, RSA77210 - Isotypes**), *R. F. Hoover 6534* (RSA43054), *K. Morse M087* (TBD), *K. Morse M117* (TBD), *K. Morse M157* (TBD), *K. Morse M158* (TBD), *K. Morse M245* (TBD), *K. Morse M246* (TBD*), *K. Morse M265* (TBD*).

Malacothamnus hallii (Eastw.) Kearney (n = 29). USA. California: Contra Costa County: *M. L. Bowerman 2223* (POM301021), *D. C. Elfving 62* (DAV54216, RSA262369), *A. D. E. Elmer 4395* (**POM61908 - Isotype of *Sphaeralcea fasciculata* var. *elmeri***), *H. M. Hall & F. M. Essig 10131* (**POM118243, UC311568 - Isotypes**), *L. S. Rose 54082* (RSA97508). Merced County: *L. P. Janeway & C. A. Janeway 1684* (DAV110593), *K. Morse M108* (TBD), *K. Morse M109* (TBD*). Santa Clara County: *L. Benson 7687* (RSA430442), *Z. E. Chandik s.n. 25 Jul 1993* (JEPS111100), *M. S. Clemens s.n. 7 Feb 1921* (CAS52631), *R. S. Ferris & R. Bacigalupi 12495* (DS341062, UC987723), *J. T. Howell 13098* (POM230338, RSA19015), *J. T. Howell 28968* (RSA88345), *M. B. Mirassou 165* (SJSU795), *J. Mo s.n. 30 May 2018* (TBD), *K. Morse M176* (TBD), *K. Morse M181* (TBD), *K. Morse M182* (TBD), *K. Morse M378* (TBD), *H. K. Sharsmith 3963* (UC1001162), *J. H. Thomas 5309* (RSA134109), *I. L. Wiggins 8518* (RSA28044). Stanislaus County: *D. W. Taylor 14961* (RSA695885).

Malacothamnus helleri (Eastw.) Kearney (n = 21). USA. California: Colusa County: *W. R. Duckworth & J. R. Keck s.n. 2 May 1976* (CDA35735), *A. A. Heller 13242* (**CAS52632 - Holotype**), *A. A. Heller s.n. 7 Jun 1940* (RSA32810), *D. Isle & F. Elliott 2134* (RSA862371), *K. Morse M105* (TBD*), *K. Morse M191* (TBD), *K. Morse M193* (TBD). Lake County: *L. Benson 4488* (POM282851), *K. Morse M106* (TBD), *K. Morse M107* (TBD*), *K. Morse M189* (TBD), *K. Morse M190* (TBD*), *K. Morse M407* (TBD), *D. Slakey et al 1* (DAV193903). Napa County: *J. Ruygt 4059* (DAV218915), *J. Ruygt 4552* (DAV218889). Solano County: *B. Crampton 894* (AHUC19274). Solano or Yolo County: *W. L. Jepson 16741* (**RSA279363 - Syntype of *Sphaeralcea fremontii* var. *exfibulosa***).

Malacothamnus howellii (Eastw.) Kearney (n = 24). USA. California: Amador County: *H. E. McMinn 5037* (UC1280814), *D. W. Taylor 11925* (JEPS101107). Calaveras County: *W. R. Howden 235* (RSA121093), *K. Morse M104* (TBD). Contra Costa County: *J. A. Ewan 8029* (POM212446), *J. T. Howell*

6470 (**POM203315, RSA434856 - Isotypes**), *J. T. Howell & T. H. Kearney 26635* (RSA127572), *K. Morse M185* (TBD), *K. Morse M186* (TBD*), *K. Morse M188* (TBD*), *K. Morse M380* (TBD*), *L. S. Rose 54081* (RSA97509). Madera County: *D. F. Schlobohm 184* (RSA121092). Mariposa County: *K. Morse & A. Colwell M239* (TBD). San Joaquin County: *J. T. Howell 48110* (AHUC36393). Santa Clara County: *E. Brooks s.n. Jul 1878* (UC138308). Stanislaus County: *A. Carter 851* (RSA77209), *C. Dudley s.n. Summer 1935* (**POM224013 - Isotype of *Malvastrum howellii* var. *cordatum***), *K. Morse M183* (TBD*).

Malacothamnus involucratus (B.L. Rob.) K. Morse (n = 34). USA. California: Monterey County: *E. K. Abbott s.n. date unknown* (CAS52722, CAS52724), *L. R. Abrams 5597* (DS68614), *L. R. Abrams 5678* (DS65611), *T. S. Brandegee s.n. date unknown* (**GH52904 - Lectotype**), *C. L. Chamberlain & L. Kiguchi s.n. 18 Jun 1982* (CAS732703), *W. R. Dudley s.n. 15 May 1895* (DS31550), *W. R. Dudley s.n. 10 Jun 1901* (DS31563), *A. Eastwood 4049* (CAS52723), *A. Eastwood s.n. Jun 1893* (**CAS744 - Syntype**), *W. I. & E. Follett s.n. 21 May 1959* (CAS420719*), *C. B. Hardham 4512* (CAS427600), *C. B. Hardham 10350* (CAS482548), *C. B. Hardham 10374* (CAS482545, RSA150729), *G. Holstein s.n. 18 Jul 2003* (DAV162441), *R. F. Hoover 4117* (DS318614), *J. T. Howell 11599* (CAS212364), *J. T. Howell & T. H. Kearney 27491* (CAS365953, GH420556), *B. F. Howitt 374* (CAS482547), *B. F. Howitt 1007* (CAS519920), *M. E. McCord s.n. date unknown* (CAS363409), *H. E. McMinn 1187* (DS164940), *K. Morse M091* (TBD*), *K. Morse M111* (TBD*), *K. Morse M382a* (TBD*), *L. S. Rose 44307* (A420563). San Luis Obispo County?: *C. Dudley s.n. 1 May 1937* (CAS265260).

Malacothamnus jonesii (Munz) Kearney (n = 22). USA. California: Monterey County: *D. Gowen 589* (RSA756409), *K. Morse M162* (TBD*), *K. Morse M382b* (TBD). San Luis Obispo County: *J. H. Barber 9235* (POM61421), *J. H. Barber s.n. date unknown* (UC55293), *C. Dudley s.n. Jun 1929* (**CAS146103 - Holotype of *Malvastrum dudleyi***), *R. S. Ferris 9763* (POM258695), *C. B. Hardham 4414* (RSA133264), *R. F. Hoover 8500* (DAV56240, RSA201702), *M. E. Jones 223* (**POM60429 - Holotype**), *M. E. Jones s.n. 25 Jun 1902* (POM85070), *K. Morse M093* (TBD), *K. Morse M094* (TBD*), *K. Morse M095* (TBD), *K. Morse M115* (TBD), *K. Morse M364* (TBD*), *K. Morse M365* (TBD), *L. S. Rose 61043* (RSA155441).

Malacothamnus lucianus (Kearney) K. Morse (n = 22). USA. California: Monterey County: *C. B. Hardham 6028* (RSA143295, SBBG17422), *C. B. Hardham 6379* (RSA139968, SBBG109832), *J. T. Howell 30642* (**CAS396253, RSA127571 - Isotypes**), *B. F. Howitt 91* (CAS580617), *A. Leary s.n. 1 Mar 1975* (CAS656827), *K. Merg & C. Clark s. n. 4 Aug 2005* (SBBG119790), *K. Morse M171* (TBD), *K. Morse M274* (TBD), *K. Morse et al M169* (TBD), *K. Morse et al M170* (TBD), *K. Morse & A. Herman M163* (TBD), *K. Morse & A. Herman M164* (TBD*), *K. Morse & A. Herman M166* (TBD*), *T. A. B. Slotta et al 2002* (CAS1085186), *D. Wilken et al 15917* (SBBG114925), *V. Yadon s.n. 6 Jul 1974* (CAS576000).

Malacothamnus marrubioides (Durand & Hilg.) Greene (n = 21). USA. California: Fresno or Los Angeles County: *A. Heerman s.n. date unknown* (**PH00016991 - Isotype**). Los Angeles County: *S. Boyd et al 8872* (RSA596432), *D. Charlton 5527* (RSA563465), *K. Morse M073* (TBD), *K. Morse M074* (TBD), *K. Morse M137* (TBD), *K. Morse M141* (TBD), *K. Morse M144* (TBD), *K. Morse M145* (TBD*), *K. Morse M286* (TBD), *K. Morse M441* (TBD), F. W. Pierson 774 (**POM9927, RSA77206 - Holotype and Isotype of *Malvastrum gabrielense*),** *F. Runyan s.n. 20 Jul 1971* (RSA434847), *P. De Vries 7771* (RSA779251), *L. C. Wheeler 10473* (RSA641493), *S. D. White et al 9628* (RSA681898), *S. D. White & A. Warniment 11228* (RSA708715), *C. B. Wolf 686* (RSA18416). Ventura County: *J. D. England & N. Fraga 1744* (RSA874167).

Malacothamnus mendocinensis (Eastw.) Kearney (n = 5). USA. California: Mendocino County: *A. Eastwood & J. T. Howell 4582* (**CAS249530 - Lectotype**), *A. Eastwood & J. T. Howell 6092* (**DS268592, POM258878 - Syntypes),** *K. Morse & J. Xerogeanes M408* (TBD), *L. S. Rose s.n. 30 May 1939* (POM259590).

Malacothamnus niveus (Eastw.) Kearney (n = 26). USA. California: Monterey County: *C. B. Hardham 6142* (RSA141034), *K. Morse M161* (TBD), *K. Morse M241* (TBD), *K. Morse M242* (TBD), *K. Morse M366* (TBD), *K. Morse M367* (TBD). San Luis Obispo County: *G. Butterworth GB2* (TBD), *G. Butterworth GB3* (TBD), *A. Eastwood & J. T. Howell 5910* (RSA22093), *C. B. Hardham 4718* (RSA133266), *C. B. Hardham & C. Butterworth 6137* (RSA141022), *J. T. Howell 24379* (RSA43315), *K. Morse M112* (TBD*), *K. Morse M116* (TBD*), *K. Morse M154* (TBD), *K. Morse M363* (TBD*), *K. Morse & G. Butterworth M432* (TBD), *E. Painter & E. Neese s.n. 16 Jun 1998* (RSA665741), *C. F. Smith 12489* (JEPS99293), *M. E. Wall s.n. 28 May 1933* (**CAS204656 - Holotype**). Santa Barbara County: *E. R. McKenzie s.n. Jun 1923* (CAS52705), *K. Morse M362* (TBD*).

Malacothamnus orbiculatus (Greene) Greene (n = 55). USA. Arizona: Mariposa County: *S. Hunkins & K. Smith 717* (AZI417438, DES70780), *S. Hunkins & K. Smith 740* (AZI417463, DES70781*), L. R. Landrum 9388* (ASU227611), *K. Morse M429*~ (TBD), *K. Morse M430* (TBD*), *K. Morse M435*~ (TBD*). Arizona: Mohave County: *G. Clifton 47274* (GLC11397). California: Inyo County: *K. Morse M221* (TBD), *K. Morse M224* (TBD), *K. Morse M226* (TBD*), *K. Morse M228* (TBD), *K. Morse M229* (TBD), *K. Morse M231* (TBD), *K. Morse M232* (TBD), *K. Morse M234* (TBD), *K. Morse M236* (TBD), *K. Morse M237* (TBD), *K. Morse M238* (TBD). Kern County*: E.L. Greene s.n. 24 Jun 1889* (**NDG31177 - Lectotype**), *K. Morse M080* (TBD), *K. Morse M206* (TBD*), *K. Morse M207* (TBD), *K. Morse M416* (TBD), *E. C. Twisselmann 8369* (RSA162535), *E. C. Twisselmann 12572* (RSA187074), *L. Yaussy s.n. 2 Jun 1937* (POM282853). Los Angeles County: *O. Mistretta 1336* (RSA589071), *K. Morse M098* (TBD), *K. Morse M128* (TBD), *K. Morse M252* (TBD), *K. Morse M253* (TBD), *K. Morse M368* (TBD), *K. Morse M369* (TBD), *K. Morse M370* (TBD*). San Bernardino County: *N. S. Fraga et al 3098* (RSA759585), *K. Morse M395* (TBD*), *K. Morse M417* (TBD), *K. Morse et al M293* (TBD*), *P. H. Raven 16625* (CAS438736). Santa Barbara County: *K. Morse M249* (TBD). Tulare County: *K. Morse M102* (TBD). Ventura County: *K. Morse M076* (TBD), *K. Morse M078* (TBD), *K. Morse M359*.

Malacothamnus palmeri (S. Watson) Greene (n = 24). USA. California: San Luis County: *J. Barber 50* (OBI51230), *J. Barber 151* (OBI51231), *A. Eastwood 15013* (A420567, CAS147741), *A. Eastwood 15027* (CAS147742), *A. Eastwood s.n. 31 Jul 1927* (POM148050), *A. Eastwood s.n. 1 Aug 1927* (RSA77205), *R. S. Ferris 9791* (A420566), *J. B. Feudge 1705* (POM147876), *C. B. Hardham 1254* (CAS508059), *G. K. Helmkamp 1215* (RSA601206), *R. F. Hoover 6200* (OBI12349, RSA43055), *R. F. Hoover 8356* (OBI12348), *D. R. Miller 604* (OBI65283), *D. R. Miller & E. A. Appel 611* (OBI75714), *K. Morse M092* (TBD), *K. Morse M243* (TBD*), *K. Morse M244* (TBD), *E. D. Palmer 50* (**GH52909 - Holotype**), *Y. Whilton s.n. 28 Jun 1933* (CAS214211), *D. Wilken & E. Painter 15932* (SBBG114965), *C. B. Wolf 2315* (RSA3059).

Malacothamnus parishii (Eastw.) Kearney (n = 3). USA. California: San Bernardino County: *S. B. Parish 3804* (**CAS52756, GH420468 - Holotype and Isotype**), *S. B. Parish 7136* (RSA433324).

"Baja east" (n = 6). MEXICO. Baja California: *R. Dominguez Cadena 4122* (SD234448), *R. Moran 13578* (SD63435), *R. Moran 14427* (RSA225211, SD79722), *R. Moran 24049* (SD97104), *R. Moran 27712* (SD103022).

"Baja east/*fasciculatus* intermediates" (n = 7). MEXICO. Baja California: *R. Moran 14542* (SD68186), *R. Moran 15499* (SD68882), *R. Moran 18043* (SD76526), *R. Moran 23413* (SD96879), *J. D. Olmstead 4672* (RSA171346), *G. Robertson 55* (UC67016), *I. L. Wiggins 9189* (DS258576).

"***fasciculatus/foliosus* intermediates"** (n = 19). MEXICO. Baja California: *J. Campos KM84* (TBD), *J. Campos KM86.8* (TBD), *A. Carter 3186* (SD176811), *A. Carter 3189* (SD176810), *F. F. Gander 7353* (SD24861), *J. T. Howell 30952* (SD71992), *R. Marin M71-90* (SD127928), *R. Moran 13204* (SD62927), *R. Moran 16201* (SD71977), *R. Moran 21032* (SD83853), *R. Moran 22525* (SD91822), *R. Moran 24375*

(SD97836), *R. Moran 24380* (SD97838), *K. Morse & J. Riley M357* (TBD*), *J. P. Rebman 3955* (SD144363), *J. P. Rebman et al 22817* (TBD), *S. Vanderplank CO-6* (SD254038), *I. L. Wiggins 11875* (SD47283).

"Santa Rosa Mountains" (n = 2). USA. California: Riverside County: *E. C. Jaeger s.n. 25 Jul 1949* (RSA50571), *R. S. Woglum 1192* (RSA95329).

"Shasta" (n = 10). USA. California: Shasta County: *B. Burgard 21~* (TBD), *Collector unknown s.n. date unknown* (AHUC18820), *K. Morse M194* (TBD), *K. Morse M197* (TBD), *K. Morse M198* (RSA898960), *K. Morse M410* (TBD), *K. Morse M412* (TBD), *K. Morse M413* (TBD), *J. P. Smith & J. O. Sawyer s.n. 1 Jun 1975* (HSC46383), *R. Tofsrud s.n. Jun 1949* (AHUC18819).

"Vandenberg" (n = 13). USA. California: Santa Barbara County: *A. P. Griffiths 18245* (CDA17924, DAV222577*, OBI66675, RSA654733), *K. Morse M398* (TBD), *K. Morse M403* (TBD*), *R. A. Nichols 664* (CAS951514, RSA628654, SBBG84140), *T. Oberbauer s.n. 21 May 1975* (SBBG72788), *T. Oberbauer s.n. 14 Jun 1977* (RSA518095).

Additional intermediates. USA. California: "*densiflorus/fasciculatus* intermediates" (n = 3). San Diego County: *A. Herman M035* (TBD), *K. Morse M002* (TBD), *K. Morse M005* (TBD). "*fremontii/orbiculatus* intermediates" (n = 2). Tulare County: *J. Stewart 751* (RSA807002), *J. Stewart & C. Capone 2102* (RSA803215). "*niveus/gracilis* intermediates" (n = 2). Santa Barbara County County: *K. Morse M247* (TBD), *K. Morse M248* (TBD). "*niveus/jonesii* intermediates" (n = 2). San Luis Obispo County: *C. B. Hardham 6983* (RSA160013), *A. Herman s.n. 13 Jun 2019* (TBD). "*orbiculatus/nuttallii* intermediate" (n = 1). Santa Barbara County: *G. F. Hrusa 16666* (CDA30544).

Appendix 2 - PCA Loadings

PCA loadings of morphological characters measured for all PCAs and axes shown in figures. The five most extreme character loadings for each axis plus any equal to the fifth most extreme are shown in bold. Dashes indicate characters excluded from a particular PCA when all included specimens had the same character value.

	Fig. 4	Fig. 4	Fig. 5	Fig. 5	Fig. 6	Fig. 6	Fig. 7	Fig. 7	Fig. 8	Fig. 8	Fig. 9	Fig. 9
Character	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**
Inflorescence longest internode	0.01	-0.05	0.02	0.05	-0.10	0.04	0.04	-0.08	0.07	-0.07	-0.06	0.06
Inflorescence longest internode length	-0.13	0.02	0.14	0.15	0.15	-0.26	0.16	0.05	-0.16	-0.02	0.10	-0.19
Inflorescence longest branch length	0.05	-0.24	-0.06	-0.03	-0.12	-0.45	-0.13	0.13	0.18	-0.14	-0.14	0.12
Inflorescence type	0.06	**-0.26**	-0.10	-0.01	-0.09	-0.44	-0.16	0.15	0.23	-0.06	-0.20	0.19
Corollas drying	—	—	—	—	—	—	—	—	—	—	—	—
Calyx length	-0.21	-0.19	**0.29**	0.05	**0.31**	0.13	**0.34**	-0.16	0.05	**-0.39**	0.26	0.18
Calyx lobe length	-0.19	-0.23	**0.29**	0.09	**0.32**	0.08	**0.36**	-0.04	0.02	**-0.38**	0.24	**0.26**
Calyx lobe width at widest	-0.05	**-0.29**	**0.25**	-0.03	**0.27**	-0.08	0.07	-0.22	0.09	**-0.38**	0.15	**0.44**
Calyx lobe width at base	-0.10	0.03	0.17	-0.15	0.18	-0.13	0.01	**-0.28**	0.11	**-0.36**	0.15	**0.44**
Calyx lobe base to widest area	-0.08	**-0.25**	0.22	0.13	0.21	0.10	0.13	0.01	-0.04	-0.11	—	—
Calyx lobe distance from tip where 1mm wide	-0.20	-0.18	0.23	0.07	0.23	0.06	0.24	0.00	-0.05	-0.22	0.20	0.17
Calyx bract length	**-0.22**	-0.04	**0.30**	0.06	**0.33**	-0.05	**0.34**	-0.11	-0.23	**-0.28**	**0.29**	0.00
Calyx bract width	0.01	0.12	0.19	-0.03	0.16	-0.16	0.07	-0.19	-0.04	-0.10	0.13	0.14
Calyx bract color	0.10	-0.14	-0.22	-0.11			-0.16	-0.09	-0.10	0.00	0.11	**-0.26**
Calyx trichomes ray length short	-0.12	-0.08	—	—	—	—	—	—	—	—	—	—
Calyx trichomes ray length long	**-0.25**	0.07	0.23	0.11	**0.29**	-0.11	**0.33**	-0.07	**-0.33**	-0.15	**0.28**	-0.09
Calyx trichomes ray length mean	-0.16	-0.09	0.10	0.20	**0.27**	0.00	**0.27**	0.03	**-0.31**	-0.13	**0.27**	-0.01
Calyx trichomes glandular short	-0.21	0.17	0.05	-0.03	—	—	—	—	—	—	—	—
Calyx trichomes glandular long	**-0.26**	0.10	0.22	-0.05	0.01	-0.36	—	—	-0.07	-0.02	—	—
Calyx trichomes glandular mean	**-0.24**	0.15	0.12	-0.03	0.02	-0.23	—	—	-0.09	-0.02	—	—
Calyx lobes with ridgelike veins	0.00	0.00	-0.03	-0.07	-0.05	0.18	0.08	-0.01	-0.09	0.01	0.11	-0.02
Simple bifurcate abaxial	-0.13	-0.05	—	—	—	—	—	—	—	—	—	—
Calyx lobe surface visible	-0.21	-0.07	-0.02	0.11	0.11	0.08	-0.01	0.20	-0.07	0.01	—	—
Calyx tube surface visible	-0.13	-0.06	-0.05	0.21	—	—	0.04	0.23	—	—	—	—
Stipular bract length	**-0.22**	0.00	**0.25**	0.08	0.23	-0.19	0.19	0.07	-0.27	-0.12	**0.27**	-0.04
Stipular bract width	-0.02	0.14	**0.27**	0.06	0.21	0.06	0.19	-0.02	-0.07	-0.20	0.06	0.08
Stem trichomes ray length short	-0.08	-0.23	-0.18	-0.04								
Stem trichomes ray length long	**-0.22**	0.04	-0.21	0.09	0.11	-0.08	-0.12	0.10	**-0.33**	-0.04	**0.29**	-0.04
Stem trichomes ray length mean	-0.09	**-0.26**	—	—	0.12	0.18	-0.13	**0.27**	**-0.34**	-0.02	**0.28**	0.02
Stem trichomes glandular short	-0.20	0.17	-0.02	0.10	—	—	—	—	—	—	—	—
Stem trichomes glandular long	-0.21	0.12	—	—	—	—	0.04	0.09	-0.05	0.00	—	—
Stem trichomes glandular mean	-0.21	0.16	-0.10	0.01	—	—	—	—	—	—	—	—
Stem trichomes rays visible to naked eye	-0.19	-0.19	-0.05	**0.43**	—	—	-0.12	0.13	**-0.29**	-0.02	**0.27**	0.00
Green stem visible to naked eye near inflorescence base	-0.21	0.11	-0.14	**0.36**	—	—	0.27	0.25	-0.11	-0.03	—	—
Green stem visible to naked eye distally in inflorescence	-0.20	-0.01	0.07	0.05	—	—	0.09	**0.37**	-0.11	0.02	—	—
Leaf trichomes adaxial mean	-0.17	0.08	-0.16	0.26	0.15	0.02	0.03	0.04	0.04	-0.21	0.21	-0.17
Leaf trichomes abaxial mean	-0.17	-0.11	-0.08	-0.01	-0.16	-0.15	0.06	**0.35**	-0.25	0.08	0.19	-0.18
Leaf lobing	0.06	0.08	0.03	**-0.41**	-0.05	-0.20	-0.13	0.00	0.16	-0.17	-0.06	0.18
Leaf cordate	-0.02	**0.25**	-0.10	0.19	0.03	0.13	-0.15	-0.26	0.16	-0.12	-0.10	**0.29**
Leaf truncate	0.04	-0.21	-0.04	**0.41**	-0.24	0.23	0.04	0.25	-0.11	0.18	0.06	**-0.27**
Leaf cuneate	0.02	**-0.29**	-0.04	**-0.42**	-0.08	-0.04	0.16	**0.27**	-0.15	0.12	0.14	-0.20

	Fig. 11	Fig. 11	Fig. 12	Fig. 12	Fig. 13	Fig. 13	Fig. 14	Fig. 14	Fig. 15	Fig. 15	Fig. 16	Fig. 16
Character	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**
Inflorescence longest internode	-0.03	0.04	-0.04	0.08	0.02	-0.03	0.02	-0.09	0.09	-0.20	-0.05	0.00
Inflorescence longest internode length	0.10	0.17	-0.15	-0.07	0.11	-0.14	0.21	0.10	0.13	-0.15	0.00	-0.16
Inflorescence longest branch length	-0.16	0.11	0.14	-0.14	-0.13	**-0.28**	0.25	0.13	0.01	**-0.26**	0.00	**-0.29**
Inflorescence type	-0.23	0.03	0.17	-0.16	-0.22	-0.24	0.24	0.05	0.11	-0.18	-0.01	**-0.25**
Corollas drying	—	—	—	—	—	—	—	—	—	—	—	—
Calyx length	-0.16	**0.33**	**-0.34**	0.14	-0.04	**-0.44**	**0.37**	-0.01	**0.35**	0.04	-0.13	**-0.42**
Calyx lobe length	-0.06	**0.30**	**-0.36**	0.01	-0.01	**-0.39**	**0.30**	-0.11	**0.30**	0.03	-0.19	**-0.33**
Calyx lobe width at widest	-0.06	**0.36**	-0.07	0.25	0.10	**-0.34**	0.26	0.24	-0.06	0.03	**-0.26**	**-0.23**
Calyx lobe width at base	-0.11	**0.33**	-0.01	**0.30**	0.08	**-0.33**	**0.27**	0.25	-0.05	-0.07	-0.23	-0.22
Calyx lobe base to widest area	0.12	0.10	-0.13	-0.01	0.10	-0.05	0.01	0.00	-0.03	0.22	—	—
Calyx lobe distance from tip where 1mm wide	-0.06	0.13	-0.24	-0.03	-0.03	-0.21	0.15	-0.23	0.24	0.21	0.02	-0.22
Calyx bract length	0.23	**0.30**	**-0.35**	0.10	**0.33**	-0.13	**0.29**	-0.16	**0.28**	0.00	-0.24	-0.17
Calyx bract width	0.09	0.21	-0.08	0.19	0.17	-0.11	0.11	-0.08	0.02	0.05	-0.16	-0.05
Calyx bract color	0.07	0.05	0.16	0.10	0.14	0.05	0.05	0.14	-0.09	0.18	-0.07	0.07
Calyx trichomes ray length short	—	—	—	—	—	—	—	—	—	—	—	—
Calyx trichomes ray length long	**0.32**	0.21	**-0.33**	0.05	**0.38**	-0.02	0.21	**-0.30**	**0.28**	**0.32**	**-0.32**	0.05
Calyx trichomes ray length mean	**0.34**	0.14	**-0.27**	-0.06	**0.35**	-0.01	0.18	**-0.33**	0.26	**0.32**	**-0.30**	0.03
Calyx trichomes glandular short	—	—	—	—	—	—	—	—	—	—	—	—
Calyx trichomes glandular long	—	—	—	—	—	—	—	—	—	—	—	—
Calyx trichomes glandular mean	—	—	—	—	—	—	—	—	—	—	—	—
Calyx lobes with ridgelike veins	-0.08	0.10	-0.09	-0.03	0.00	-0.14	0.09	**-0.26**	**0.29**	-0.10	-0.03	-0.19
Simple bifurcate abaxial	—	—	—	—	—	—	—	—	—	—	—	—
Calyx lobe surface visible	0.21	-0.11	0.01	-0.20	0.10	0.13	-0.11	0.00	0.02	-0.21	-0.15	0.21
Calyx tube surface visible	0.12	-0.10	—	—	—	—	—	—	—	—	—	—
Stipular bract length	0.16	0.23	-0.18	-0.07	0.23	-0.15	0.17	-0.12	0.22	0.01	**-0.26**	-0.11
Stipular bract width	0.10	0.29	-0.19	0.01	0.19	-0.21	0.26	0.10	0.06	0.02	-0.23	-0.08
Stem trichomes ray length short	—	—	—	—	—	—	—	—	—	—	—	—
Stem trichomes ray length long	**0.33**	0.00	0.13	-0.11	**0.35**	0.10	0.02	**-0.30**	0.15	**0.36**	**-0.29**	0.20
Stem trichomes ray length mean	**0.33**	-0.05	0.15	**-0.28**	**0.34**	0.06	0.09	-0.22	0.09	**0.32**	-0.25	0.15
Stem trichomes glandular short	—	—	—	—	—	—	—	—	—	—	—	—
Stem trichomes glandular long	0.10	-0.02	-0.03	-0.09	—	—	—	—	—	—	—	—
Stem trichomes glandular mean	—	—	—	—	—	—	—	—	—	—	—	—
Stem trichomes rays visible to naked eye	0.17	-0.05	0.13	-0.14	0.13	-0.01	0.09	-0.04	—	—	—	—
Green stem visible to naked eye near inflorescence base	0.22	-0.01	-0.26	-0.26	—	—	—	—	—	—	—	—
Green stem visible to naked eye distally in inflorescence	0.26	-0.11	-0.08	**-0.37**	0.01	0.02	—	—	—	—	—	—
Leaf trichomes adaxial mean	-0.01	0.20	-0.03	-0.05	0.13	-0.11	**0.28**	0.08	0.19	-0.25	-0.28	0.18
Leaf trichomes abaxial mean	**0.28**	-0.10	-0.04	**-0.36**	0.15	0.10	-0.09	**-0.34**	**0.32**	-0.12	-0.22	0.22
Leaf lobing	-0.10	0.10	0.14	0.02	0.00	-0.14	0.22	0.25	-0.09	0.02	0.01	-0.11
Leaf cordate	-0.03	0.07	0.14	0.26	0.12	0.14	-0.04	0.19	-0.19	0.20	-0.08	0.20
Leaf truncate	0.00	-0.18	-0.03	-0.26	-0.18	0.04	-0.03	-0.21	0.20	-0.21	0.26	-0.03
Leaf cuneate	-0.04	-0.10	-0.15	**-0.28**	-0.19	-0.13	0.07	-0.18	0.25	-0.22	0.20	**-0.23**

	Fig. 17	Fig. 17	Fig. 18	Fig. 18	Fig. 19	Fig. 19	Fig. 23	Fig. 23	Fig. 24	Fig. 24	Fig. 26	Fig. 26
Character	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**
Inflorescence longest internode	-0.10	0.06	-0.06	0.08	0.02	-0.13	0.09	-0.01	0.06	-0.08	0.12	0.03
Inflorescence longest internode length	-0.16	-0.05	0.01	-0.02	-0.05	-0.07	0.07	0.15	-0.01	0.18	-0.09	**0.27**
Inflorescence longest branch length	-0.10	-0.25	-0.14	-0.02	0.22	-0.11	0.00	0.11	-0.06	0.12	-0.11	-0.21
Inflorescence type	-0.03	**-0.29**	-0.19	-0.06	0.27	-0.14	-0.01	0.06	-0.07	0.10	-0.11	-0.13
Corollas drying	—	—	—	—	—	—	—	—	—	—	—	—
Calyx length	-0.24	**-0.35**	-0.23	**0.38**	0.14	**-0.43**	-0.03	**0.35**	0.11	**0.32**	-0.25	0.12
Calyx lobe length	**-0.31**	-0.21	**-0.26**	**0.42**	0.09	**-0.46**	0.14	**0.37**	0.09	**0.34**	**-0.28**	0.07
Calyx lobe width at widest	-0.26	-0.17	-0.23	-0.07	0.11	-0.11	-0.22	0.23	0.03	0.12	-0.02	0.19
Calyx lobe width at base	-0.21	-0.18	-0.18	-0.11	0.12	-0.07	-0.20	**0.27**	0.11	0.04	0.01	0.20
Calyx lobe base to widest area	—	—	-0.13	0.11	—	—	0.01	-0.02	-0.09	0.16	-0.06	0.15
Calyx lobe distance from tip where 1mm wide	-0.16	-0.19	-0.13	**0.41**	-0.03	**-0.37**	0.09	0.21	0.10	0.26	**-0.26**	-0.10
Calyx bract length	**-0.32**	-0.08	**-0.31**	-0.03	**-0.31**	-0.15	-0.17	0.24	0.00	**0.36**	**-0.30**	0.08
Calyx bract width	-0.16	0.00	-0.11	-0.08	-0.08	-0.04	0.13	0.08	-0.10	0.00	0.04	0.15
Calyx bract color	0.13	-0.04	-0.10	-0.28	-0.17	0.17	-0.02	0.06	-0.04	-0.05	0.00	0.05
Calyx trichomes ray length short	—	—	—	—	—	—	-0.08	-0.22	-0.11	0.16	-0.20	-0.20
Calyx trichomes ray length long	**-0.31**	0.15	**-0.34**	-0.01	**-0.37**	-0.15	**-0.29**	-0.04	0.12	**0.28**	-0.21	**0.26**
Calyx trichomes ray length mean	**-0.28**	0.14	**-0.26**	0.11	**-0.35**	-0.16	**-0.33**	0.07	-0.16	0.27	-0.25	0.16
Calyx trichomes glandular short	—	—	—	—	—	—	—	—	**0.29**	-0.05	-0.17	**-0.24**
Calyx trichomes glandular long	—	—	—	—	—	—	-0.15	**-0.27**	**0.30**	0.02	**-0.28**	0.03
Calyx trichomes glandular mean	—	—	—	—	—	—	-0.08	**-0.33**	**0.30**	0.00	-0.23	-0.01
Calyx lobes with ridgelike veins	-0.08	-0.22	-0.12	0.03	-0.09	-0.17	0.13	0.15	0.05	0.08	-0.03	0.03
Simple bifurcate abaxial	—	—	—	—	—	—	—	—	-0.09	0.19	-0.15	0.14
Calyx lobe surface visible	-0.04	0.17	-0.08	-0.20	-0.11	0.09	0.07	-0.16	-0.02	0.19	-0.16	-0.04
Calyx tube surface visible	—	—	—	—	—	—	—	—	-0.22	0.19	-0.19	0.03
Stipular bract length	-0.27	-0.06	**-0.29**	-0.12	-0.23	-0.15	-0.16	-0.21	0.12	**0.30**	**-0.29**	0.03
Stipular bract width	**-0.30**	0.07	-0.23	-0.01	-0.03	-0.14	-0.04	-0.21	0.05	0.05	-0.06	-0.05
Stem trichomes ray length short	—	—	—	—	—	—	-0.12	-0.06	0.01	0.16	-0.14	-0.18
Stem trichomes ray length long	-0.12	0.20	-0.25	-0.07	**-0.37**	-0.05	**-0.35**	0.11	0.26	0.06	-0.15	0.03
Stem trichomes ray length mean	-0.13	0.11	-0.25	-0.02	**-0.37**	-0.06	**-0.32**	0.09	0.09	0.10	-0.17	**-0.25**
Stem trichomes glandular short	—	—	—	—	—	—	—	—	**0.29**	-0.04	—	—
Stem trichomes glandular long	—	—	—	—	—	—	-0.23	-0.07	**0.31**	-0.07	-0.12	-0.20
Stem trichomes glandular mean	—	—	—	—	—	—	-0.16	-0.04	**0.31**	-0.05	-0.16	-0.18
Stem trichomes rays visible to naked eye	—	—	—	—	—	—	-0.26	-0.03	0.12	0.12	-0.16	-0.07
Green stem visible to naked eye near inflorescence base	—	—	—	—	—	—	0.02	0.05	0.17	0.06	-0.14	0.21
Green stem visible to naked eye distally in inflorescence	—	—	—	—	—	—	0.07	0.09	0.17	0.06	-0.09	0.22
Leaf trichomes adaxial mean	-0.18	**0.28**	-0.20	-0.12	0.15	-0.13	-0.26	0.10	0.15	0.02	-0.05	**0.27**
Leaf trichomes abaxial mean	-0.17	**0.29**	-0.09	-0.01	-0.18	-0.14	**-0.28**	-0.02	0.18	-0.01	0.05	0.21
Leaf lobing	0.10	-0.23	-0.14	**-0.31**	0.04	0.14	-0.08	0.13	0.02	-0.07	0.06	-0.09
Leaf cordate	-0.02	0.25	-0.01	-0.27	-0.10	**0.26**	—	—	0.08	-0.01	-0.05	-0.10
Leaf truncate	0.23	-0.12	0.21	0.12	0.07	-0.05	0.04	-0.13	-0.17	0.10	-0.02	**0.24**
Leaf cuneate	0.12	**-0.33**	0.07	**0.33**	0.11	**-0.28**	0.01	0.00	-0.12	0.05	0.04	0.19

	Fig. 27	Fig. 27	Fig. 28	Fig. 28	Fig. 29	Fig. 29	Fig. 30	Fig. 30	Fig. 33	Fig. 33	Fig. 33	Fig. 34	Fig. 34
Character	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**	**PC3**	**PC1**	**PC2**
Inflorescence longest internode	0.05	-0.18	-0.11	0.08	0.05	-0.02	0.05	0.12	0.07	0.09	0.02	—	—
Inflorescence longest internode length	**0.24**	0.12	**0.32**	0.25	0.14	0.15	-0.04	**0.24**	0.04	-0.11	-0.03	0.19	-0.20
Inflorescence longest branch length	-0.22	0.02	0.09	-0.01	0.20	-0.09	0.18	0.21	0.03	-0.13	-0.01	-0.08	-0.25
Inflorescence type	-0.15	0.06	-0.08	-0.04	0.20	-0.18	**0.25**	0.15	0.06	-0.18	-0.08	-0.15	-0.16
Corollas drying	—	—	—	—	—	—	—	—	0.04	**-0.31**	-0.14	-0.22	-0.01
Calyx length	0.05	**0.29**	-0.13	**0.34**	-0.06	**0.32**	-0.20	0.04	-0.22	-0.13	-0.06	0.00	**-0.38**
Calyx lobe length	-0.01	**0.31**	-0.14	**0.37**	-0.04	**0.33**	-0.21	0.01	-0.22	-0.10	-0.02	0.06	**-0.36**
Calyx lobe width at widest	0.17	0.09	-0.13	0.02	0.22	-0.03	0.16	-0.06	-0.10	-0.16	**-0.27**	**0.28**	-0.09
Calyx lobe width at base	0.19	0.05	-0.12	0.10	0.01	0.04	-0.03	-0.18	-0.12	-0.20	-0.22	0.01	-0.16
Calyx lobe base to widest area	0.12	0.16	0.01	-0.14	0.16	0.17	-0.09	0.13	-0.06	-0.05	-0.19	**0.25**	-0.16
Calyx lobe distance from tip where 1mm wide	-0.16	0.23	-0.15	**0.30**	-0.12	**0.28**	-0.24	0.14	-0.15	-0.07	0.15	-0.10	-0.13
Calyx bract length	0.00	**0.33**	0.04	**0.32**	-0.22	0.13	-0.24	-0.03	-0.16	**-0.33**	-0.06	-0.03	**-0.38**
Calyx bract width	0.15	-0.01	0.11	0.09	-0.15	0.02	-0.05	-0.01	-0.06	-0.19	-0.04	-0.14	-0.14
Calyx bract color	0.06	-0.05	-0.09	-0.12	0.18	-0.11	0.17	-0.09	-0.15	-0.13	-0.16	-0.22	-0.03
Calyx trichomes ray length short	**-0.25**	0.13	—	—	0.07	0.22	-0.10	0.18	-0.11	-0.06	0.18	-0.15	0.14
Calyx trichomes ray length long	0.22	0.25	**0.29**	0.05	**-0.24**	0.14	**-0.27**	-0.19	-0.17	**-0.24**	0.10	**-0.25**	-0.05
Calyx trichomes ray length mean	0.11	**0.28**	**0.36**	0.15	-0.04	0.20	-0.17	**-0.27**	-0.14	**-0.27**	0.19	**-0.27**	-0.09
Calyx trichomes glandular short	**-0.27**	0.10	0.22	0.16	-0.21	0.01	-0.12	**0.32**	-0.25	0.19	-0.14	-0.09	0.08
Calyx trichomes glandular long	-0.04	0.26	0.25	0.17	**-0.26**	0.06	**-0.27**	0.04	**-0.27**	0.04	-0.12	**-0.27**	-0.01
Calyx trichomes glandular mean	-0.07	0.20	**0.29**	0.24	**-0.27**	0.01	-0.21	0.21	**-0.27**	0.13	-0.13	-0.21	-0.01
Calyx lobes with ridgelike veins	0.02	0.02	0.05	-0.11	-0.20	-0.02	-0.07	0.08	0.05	**-0.25**	-0.14	-0.01	-0.07
Simple bifurcate abaxial	0.11	0.16	—	—	—	—	—	—	—	—	—	—	—
Calyx lobe surface visible	-0.08	0.03	—	—	**0.26**	0.07	0.07	0.23	-0.10	0.22	-0.13	0.23	-0.04
Calyx tube surface visible	-0.01	0.09	—	—	—	—	—	—	0.04	0.13	0.02	—	—
Stipular bract length	-0.05	**0.30**	0.11	0.15	-0.20	0.10	-0.18	-0.02	-0.18	-0.23	-0.04	-0.14	**-0.28**
Stipular bract width	-0.06	0.03	0.05	0.12	-0.07	-0.05	0.04	-0.12	0.05	0.03	0.06	-0.09	-0.15
Stem trichomes ray length short	-0.21	0.09	—	—	0.18	0.14	-0.03	0.02	-0.09	0.17	0.18	0.13	-0.13
Stem trichomes ray length long	0.00	0.11	0.18	**-0.29**	0.09	**0.23**	-0.20	-0.19	-0.20	-0.06	**0.30**	-0.23	-0.09
Stem trichomes ray length mean	**-0.28**	0.08	0.23	-0.20	0.17	0.16	-0.09	**-0.35**	-0.20	-0.04	**0.33**	-0.23	-0.07
Stem trichomes glandular short	—	—	—	—	0.04	0.19	-0.12	**0.32**	-0.24	0.21	-0.15	—	—
Stem trichomes glandular long	-0.22	0.09	0.03	-0.03	0.02	0.22	**-0.26**	0.00	**-0.26**	0.18	-0.14	-0.10	-0.06
Stem trichomes glandular mean	-0.21	0.13	0.14	0.01	0.07	**0.34**	**-0.26**	0.18	**-0.25**	0.20	-0.15	-0.09	0.08
Stem trichomes rays visible to naked eye	-0.11	0.06	0.07	-0.11	0.20	0.15	-0.07	-0.22	-0.15	-0.10	**0.33**	-0.18	-0.08
Green stem visible to naked eye near inflorescence base	0.15	0.25	—	—	—	—	—	—	-0.05	0.03	-0.15	**0.26**	0.01
Green stem visible to naked eye distally in inflorescence	0.19	0.14	—	—	0.21	-0.18	0.24	0.10	-0.12	0.07	-0.11	0.15	-0.05
Leaf trichomes adaxial mean	**0.25**	0.07	**0.30**	-0.13	0.19	0.07	0.03	-0.16	**-0.25**	0.03	-0.02	0.14	**-0.28**
Leaf trichomes abaxial mean	0.22	-0.05	0.20	-0.25	**0.27**	0.07	0.09	-0.01	-0.20	-0.05	0.11	0.06	-0.24
Leaf lobing	-0.07	-0.10	0.25	-0.04	0.05	-0.02	0.05	0.13	-0.12	0.03	-0.03	0.03	-0.12
Leaf cordate	-0.11	0.06	0.09	0.00	-0.12	-0.20	0.16	-0.07	-0.10	0.09	**0.25**	0.08	0.04
Leaf truncate	0.22	0.05	0.08	0.00	0.04	-0.16	0.17	-0.05	0.12	-0.09	-0.18	-0.03	-0.06
Leaf cuneate	0.20	-0.05	0.11	0.18	0.11	0.17	-0.14	0.03	0.11	-0.09	-0.19	-0.08	-0.02

	Fig. 35	Fig. 35	Fig. 36	Fig. 36	Fig. 37	Fig. 37	Fig. 38	Fig. 38	Fig. 42	Fig. 42	Fig. 43	Fig. 43
Character	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**
Inflorescence longest internode	0.08	0.03	0.07	-0.14	-0.12	0.01	0.07	-0.15	0.03	-0.04	0.04	0.12
Inflorescence longest internode length	0.01	0.12	0.07	0.09	0.00	0.12	-0.06	-0.03	0.00	-0.17	0.14	0.12
Inflorescence longest branch length	-0.05	0.12	0.05	0.13	0.10	-0.02	-0.10	-0.12	0.23	-0.09	0.10	**0.33**
Inflorescence type	-0.11	0.16	0.02	0.09	0.09	0.11	-0.18	-0.04	0.17	-0.11	0.10	**0.34**
Corollas drying	**-0.25**	-0.12	**-0.28**	-0.17	—	—	0.06	0.08	—	—	—	—
Calyx length	-0.20	**0.32**	-0.04	**0.23**	0.19	**0.33**	**-0.28**	0.21	**0.26**	-0.19	0.23	0.23
Calyx lobe length	-0.17	**0.31**	0.00	**0.34**	0.25	0.21	-0.25	**0.29**	**0.28**	-0.15	0.21	0.28
Calyx lobe width at widest	-0.21	0.05	**-0.24**	**-0.24**	-0.03	**0.47**	-0.13	-0.25	0.15	-0.18	0.18	-0.08
Calyx lobe width at base	-0.21	0.03	-0.23	**-0.23**	-0.02	**0.46**	-0.15	**-0.28**	0.11	-0.18	0.17	-0.12
Calyx lobe base to widest area	-0.04	0.13	-0.06	-0.10	-0.09	0.03	0.01	0.05	0.14	-0.09	0.11	0.09
Calyx lobe distance from tip where 1mm wide	-0.11	0.22	0.07	**0.37**	0.23	**-0.23**	-0.19	**0.32**	0.25	-0.05	0.08	**0.37**
Calyx bract length	**-0.28**	0.14	**-0.24**	0.16	0.26	0.18	**-0.32**	0.10	0.13	**-0.27**	**0.25**	0.13
Calyx bract width	-0.15	0.08	-0.12	-0.11	-0.04	**0.30**	-0.18	-0.07	**0.29**	-0.08	0.19	0.00
Calyx bract color	-0.23	-0.12	**-0.26**	-0.17	-0.02	-0.15	-0.12	-0.26	**-0.26**	0.07	-0.11	0.13
Calyx trichomes ray length short	-0.11	-0.12	-0.19	0.18	0.24	0.06	-0.03	-0.08	-0.05	-0.24	0.20	0.07
Calyx trichomes ray length long	**-0.27**	-0.10	**-0.29**	0.15	**0.31**	0.03	**-0.28**	-0.10	-0.17	**-0.31**	**0.29**	-0.03
Calyx trichomes ray length mean	**-0.27**	-0.10	**-0.29**	0.15	**0.31**	-0.01	**-0.28**	-0.11	-0.19	**-0.32**	**0.31**	-0.02
Calyx trichomes glandular short	-0.09	0.12	—	—	—	—	—	—	0.30	0.06	-0.11	0.26
Calyx trichomes glandular long	**-0.25**	0.13	-0.19	-0.19	-0.10	0.00	-0.27	0.13	0.24	0.07	-0.08	**0.32**
Calyx trichomes glandular mean	-0.23	0.17	-0.18	**-0.23**	-0.14	0.07	-0.23	0.12	**0.29**	0.13	-0.15	**0.35**
Calyx lobes with ridgelike veins	-0.17	0.07	-0.13	-0.03	0.06	0.17	-0.17	0.09	0.04	-0.01	0.02	-0.03
Simple bifurcate abaxial	—	—	—	—	—	—	—	—	—	—	—	—
Calyx lobe surface visible	0.14	0.17	0.16	-0.04	-0.12	-0.01	0.20	0.18	0.00	0.20	-0.19	0.23
Calyx tube surface visible	0.10	0.18	0.13	-0.05	-0.12	-0.10	—	—	—	—	—	—
Stipular bract length	**-0.25**	0.11	-0.19	-0.01	0.07	-0.06	**-0.28**	0.14	0.15	-0.17	0.18	-0.04
Stipular bract width	0.06	**0.28**	0.15	0.01	-0.07	0.08	-0.21	0.06	0.23	-0.07	0.13	-0.04
Stem trichomes ray length short	0.08	-0.21	-0.03	0.22	0.20	-0.16	0.18	-0.02	—	—	—	—
Stem trichomes ray length long	-0.19	**-0.28**	-0.21	0.22	**0.31**	-0.08	-0.03	0.01	-0.05	**-0.30**	**0.26**	-0.02
Stem trichomes ray length mean	-0.18	**-0.30**	-0.22	**0.23**	**0.31**	-0.12	-0.02	-0.13	-0.10	**-0.31**	**0.29**	-0.05
Stem trichomes glandular short	—	—	—	—	—	—	—	—	—	—	—	—
Stem trichomes glandular long	-0.15	0.05	-0.16	-0.03	—	—	-0.11	0.08	—	—	—	—
Stem trichomes glandular mean	-0.10	0.07	—	—	—	—	-0.07	-0.01	—	—	—	—
Stem trichomes rays visible to naked eye	-0.17	-0.25	-0.23	**0.23**	**0.33**	-0.09	0.03	-0.01	-0.02	-0.12	0.10	0.00
Green stem visible to naked eye near inflorescence base	0.05	0.01	0.03	0.06	0.04	-0.17	—	—	—	—	—	—
Green stem visible to naked eye distally in inflorescence	-0.01	-0.04	0.02	-0.01	0.02	-0.15	0.03	-0.02	—	—	—	—
Leaf trichomes adaxial mean	-0.13	-0.15	-0.19	0.02	0.16	0.03	-0.11	**-0.28**	-0.12	**-0.27**	**0.25**	0.05
Leaf trichomes abaxial mean	-0.13	-0.22	-0.20	0.01	0.16	0.08	-0.08	-0.26	-0.18	-0.25	0.24	-0.03
Leaf lobing	-0.05	-0.13	-0.08	0.05	0.09	0.07	0.13	0.27	0.20	-0.03	0.02	0.12
Leaf cordate	0.06	-0.01	0.04	-0.15	-0.06	0.00	0.06	0.10	-0.01	-0.15	0.14	-0.15
Leaf truncate	-0.01	-0.02	0.01	0.05	0.00	0.01	-0.09	**-0.28**	-0.05	-0.13	0.13	-0.14
Leaf cuneate	-0.03	-0.02	0.03	0.10	0.00	-0.04	-0.08	-0.21	-0.10	0.01	-0.04	0.05

Appendix 3 - Full-genus PERMANOVA Results

PERMANOVA results from pairwise comparisons assessing the full genus *Malacothamnus* classified by the 38 morphological groups recovered in species subset analyses. Results are ordered by pseudo *F*-ratio. Insignificant *p*-values are in bold.

pairs	SumsOfSqs	pseudo-F	R2	p-value
laxiflorus vs lucianus	3.43	401.5	0.84	0.001
hallii vs lucianus	3.12	320.7	0.87	0.001
jonesii vs lucianus	3.06	285.8	0.87	0.001
fasciculatus_ss vs lucianus	2.65	278.8	0.84	0.001
lucianus vs nuttallii	3.09	266.8	0.86	0.001
lucianus vs niveus	2.90	249.4	0.84	0.001
lucianus vs orbiculatus	2.46	237.5	0.76	0.001
laxiflorus vs palmeri	2.09	236.0	0.75	0.001
helleri vs lucianus	2.90	235.8	0.85	0.001
arcuatus vs lucianus	2.68	227.5	0.84	0.001
catalinensis vs lucianus	2.36	224.1	0.85	0.001
laxiflorus vs viscidus	2.09	196.5	0.72	0.001
abbottii vs lucianus	2.46	176.8	0.82	0.001
davidsonii (south) vs lucianus	2.30	175.4	0.80	0.001
gracilis vs lucianus	2.08	164.2	0.84	0.001
lucianus vs nesioticus	2.02	163.7	0.83	0.001
davidsonii (north) vs lucianus	1.97	162.8	0.81	0.001
fasciculatus_ss vs palmeri	1.58	160.2	0.75	0.001
laxiflorus vs Vandenberg	1.51	151.1	0.69	0.001
densiflorus (SD & SA) vs laxiflorus	2.12	149.3	0.64	0.001
fasciculatus/foliosus int. vs lucianus	2.04	149.1	0.79	0.001
enigmaticus vs lucianus	1.83	147.1	0.79	0.001
hallii vs viscidus	2.03	144.0	0.75	0.001
nuttallii vs palmeri	1.62	143.1	0.76	0.001
catalinensis vs palmeri	1.48	142.7	0.77	0.001
hallii vs Vandenberg	1.63	139.5	0.78	0.001
howellii vs lucianus	2.10	137.5	0.76	0.001
foliosus (coastal) vs lucianus	2.03	134.6	0.78	0.001
hallii vs palmeri	1.36	134.0	0.72	0.001
clementinus vs lucianus	1.71	133.7	0.77	0.001
aboriginum vs lucianus	1.86	132.8	0.77	0.001
foliosus (inland) vs laxiflorus	1.52	130.0	0.64	0.001
palmeri vs viscidus	1.96	129.1	0.75	0.001
nuttallii vs viscidus	1.96	125.1	0.76	0.001
lucianus vs palmeri	1.82	123.7	0.74	0.001
niveus vs viscidus	1.97	122.8	0.74	0.001
nuttallii vs Vandenberg	1.58	122.2	0.79	0.001
involucratus vs laxiflorus	1.45	119.4	0.57	0.001
jonesii vs viscidus	1.83	119.3	0.75	0.001

pairs	SumsOfSqs	pseudo-F	R2	p-value
fremontii (south) vs lucianus	1.62	118.7	0.77	0.001
densiflorus (SJ) vs laxiflorus	1.37	117.5	0.64	0.001
jonesii vs palmeri	1.29	117.2	0.73	0.001
jonesii vs Vandenberg	1.42	116.5	0.78	0.001
lucianus vs marrubioides	1.76	116.4	0.74	0.001
howellii vs laxiflorus	1.31	116.2	0.59	0.001
palmeri vs Vandenberg	1.47	114.6	0.77	0.001
involucratus vs lucianus	1.82	112.8	0.68	0.001
fasciculatus_ss vs viscidus	1.50	111.8	0.69	0.001
helleri vs viscidus	1.95	110.7	0.74	0.001
aboriginum vs laxiflorus	1.11	109.6	0.59	0.001
nesioticus vs palmeri	1.33	109.5	0.76	0.001
foliosus (coastal) vs laxiflorus	1.23	108.5	0.60	0.001
foliosus (inland) vs lucianus	1.59	106.2	0.74	0.001
orbiculatus vs palmeri	1.42	105.4	0.58	0.001
clementinus vs laxiflorus	1.08	103.6	0.58	0.001
clementinus vs palmeri	1.53	102.4	0.71	0.001
gracilis vs palmeri	1.16	96.7	0.74	0.001
niveus vs palmeri	1.20	96.1	0.67	0.001
arcuatus vs viscidus	1.53	96.0	0.70	0.001
orbiculatus vs viscidus	1.40	94.3	0.56	0.001
helleri vs palmeri	1.19	92.6	0.68	0.001
densiflorus (SJ) vs hallii	1.42	90.1	0.70	0.001
densiflorus (SD & SA) (SD & SA) vs hallii	1.67	89.7	0.62	0.001
helleri vs Vandenberg	1.44	89.1	0.74	0.001
aboriginum vs jonesii	1.13	88.5	0.69	0.001
abbottii vs clementinus	1.39	88.0	0.70	0.001
aboriginum vs hallii	1.06	87.4	0.65	0.001
fasciculatus/foliosus int. vs palmeri	1.31	87.1	0.68	0.001
densiflorus (SD & SA) vs nuttallii	1.78	87.0	0.65	0.001
abbottii vs viscidus	1.63	86.9	0.70	0.001
howellii vs palmeri	1.27	86.8	0.65	0.001
davidsonii (north) vs palmeri	1.14	86.4	0.68	0.001
densiflorus (SJ) vs nuttallii	1.54	86.1	0.74	0.001
hallii vs howellii	1.12	85.8	0.63	0.001
davidsonii (south) vs palmeri	1.34	85.8	0.65	0.001
fasciculatus_ss vs Vandenberg	1.10	85.5	0.67	0.001
aboriginum vs nuttallii	1.10	85.3	0.68	0.001
laxiflorus vs Shasta	0.83	85.3	0.56	0.001
catalinensis vs viscidus	1.29	85.0	0.69	0.001
laxiflorus vs marrubioides	0.98	84.7	0.52	0.001
aboriginum vs niveus	1.32	84.1	0.66	0.001
laxiflorus vs niveus	0.90	83.5	0.50	0.001
densiflorus (SJ) vs jonesii	1.46	82.1	0.73	0.001

pairs	SumsOfSqs	pseudo-F	R2	p-value
enigmaticus vs palmeri	0.91	81.8	0.66	0.001
clementinus vs hallii	1.03	81.8	0.64	0.001
densiflorus (SD & SA) vs fasciculatus_ss	1.45	81.5	0.59	0.001
abbottii vs palmeri	1.08	81.0	0.66	0.001
nuttallii vs Shasta	0.96	81.0	0.73	0.001
niveus vs Vandenberg	1.32	80.2	0.68	0.001
arcuatus vs palmeri	0.95	79.2	0.64	0.001
hallii vs Shasta	0.80	78.5	0.68	0.001
densiflorus (SD & SA) vs orbiculatus	1.37	78.0	0.49	0.001
abbottii vs Vandenberg	1.36	77.6	0.71	0.001
hallii vs involucratus	1.13	77.5	0.56	0.001
aboriginum vs helleri	1.23	77.0	0.66	0.001
fremontii (south) vs palmeri	1.20	76.9	0.67	0.001
gracilis vs viscidus	1.41	76.1	0.72	0.001
howellii vs nuttallii	1.11	76.0	0.63	0.001
foliosus (inland) vs nuttallii	1.23	74.6	0.67	0.001
jonesii vs Shasta	0.89	74.5	0.71	0.001
catalinensis vs Vandenberg	0.99	74.2	0.70	0.001
howellii vs jonesii	1.04	74.1	0.63	0.001
densiflorus (SD & SA) vs palmeri	1.42	72.9	0.60	0.001
densiflorus (SD & SA) vs lucianus	1.42	72.1	0.61	0.001
aboriginum vs gracilis	1.12	72.0	0.71	0.001
fremontii (south) vs laxiflorus	0.83	71.9	0.50	0.001
arcuatus vs laxiflorus	0.72	71.9	0.48	0.001
densiflorus (SD & SA) vs jonesii	1.46	71.9	0.60	0.001
involucratus vs niveus	1.22	71.1	0.55	0.001
gracilis vs Vandenberg	1.14	70.5	0.75	0.001
involucratus vs viscidus	1.31	70.2	0.57	0.001
clementinus vs nuttallii	1.02	70.1	0.64	0.001
nesioticus vs viscidus	1.25	70.0	0.69	0.001
foliosus (inland) vs hallii	1.11	69.8	0.61	0.001
arcuatus vs Vandenberg	1.09	69.7	0.67	0.001
fasciculatus_ss vs foliosus (inland)	1.07	69.2	0.60	0.001
fasciculatus_ss vs foliosus (coastal)	0.98	68.2	0.59	0.001
davidsonii (north) vs viscidus	1.21	68.2	0.65	0.001
densiflorus (SJ) vs fasciculatus_ss	1.07	68.0	0.62	0.001
involucratus vs jonesii	1.16	68.0	0.56	0.001
davidsonii (south) vs viscidus	1.24	67.5	0.62	0.001
howellii vs viscidus	1.28	67.3	0.62	0.001
densiflorus (SD & SA) vs helleri	1.52	67.0	0.59	0.001
fasciculatus_ss vs howellii	0.86	66.6	0.55	0.001
clementinus vs jonesii	0.93	66.1	0.62	0.001
enigmaticus vs hallii	0.71	65.7	0.58	0.001
catalinensis vs densiflorus (SJ)	1.09	65.7	0.69	0.001

pairs	SumsOfSqs	pseudo-F	R2	p-value
lucianus vs Shasta	1.12	65.3	0.69	0.001
laxiflorus vs orbiculatus	0.89	65.2	0.37	0.001
foliosus (coastal) vs hallii	0.97	65.0	0.60	0.001
nesioticus vs Vandenberg	1.05	64.9	0.73	0.001
densiflorus (SD & SA) vs niveus	1.35	64.7	0.56	0.001
densiflorus (SJ) vs helleri	1.36	64.7	0.68	0.001
involucratus vs nuttallii	1.14	64.6	0.54	0.001
helleri vs involucratus	1.13	64.2	0.55	0.001
lucianus vs mendocinensis	1.03	64.1	0.72	0.001
fasciculatus/foliosus int. vs viscidus	1.21	63.7	0.63	0.001
catalinensis vs densiflorus (SD & SA)	1.29	63.6	0.58	0.001
clementinus vs niveus	0.99	63.2	0.59	0.001
densiflorus (SJ) vs niveus	1.27	63.1	0.64	0.001
fasciculatus_ss vs involucratus	0.96	62.9	0.50	0.001
foliosus (coastal) vs viscidus	1.34	62.3	0.64	0.001
densiflorus (SJ) vs palmeri	1.19	61.8	0.65	0.001
gracilis vs Shasta	0.93	61.7	0.76	0.001
"Baja East" vs lucianus	1.05	61.5	0.70	0.001
catalinensis vs foliosus (inland)	1.05	61.1	0.63	0.001
foliosus (coastal) vs nuttallii	0.98	60.6	0.62	0.001
abbottii vs fremontii (south)	1.11	60.3	0.64	0.001
abbottii vs aboriginum	1.06	60.3	0.61	0.001
fremontii (north) vs lucianus	1.08	60.2	0.69	0.001
abbottii vs laxiflorus	0.82	60.2	0.44	0.001
enigmaticus vs nuttallii	0.70	60.1	0.60	0.001
davidsonii (north) vs Vandenberg	1.00	59.9	0.67	0.001
clementinus vs gracilis	0.98	59.9	0.67	0.001
foliosus (coastal) vs palmeri	0.97	59.9	0.61	0.001
aboriginum vs fasciculatus_ss	0.68	59.8	0.54	0.001
aboriginum vs viscidus	1.07	59.7	0.61	0.001
abbottii vs densiflorus (SD & SA)	1.44	59.5	0.57	0.001
abbottii vs fasciculatus_ss	0.78	59.1	0.54	0.001
fremontii (south) vs hallii	0.84	59.0	0.58	0.001
catalinensis vs foliosus (coastal)	0.93	58.9	0.62	0.001
enigmaticus vs viscidus	1.02	58.9	0.61	0.001
"Baja East"/fasciculatus int. vs lucianus	1.05	58.7	0.68	0.001
gracilis vs involucratus	1.07	58.5	0.57	0.001
lucianus vs Vandenberg	1.05	58.3	0.64	0.001
abbottii vs orbiculatus	1.07	58.0	0.44	0.001
gracilis vs howellii	0.98	57.6	0.63	0.001
clementinus vs viscidus	0.95	57.4	0.60	0.001
clementinus vs marrubioides	0.88	57.4	0.60	0.001
marrubioides vs palmeri	0.81	56.7	0.57	0.001
clementinus vs helleri	0.97	56.3	0.59	0.001

pairs	SumsOfSqs	pseudo-F	R2	p-value
involucratus vs orbiculatus	0.84	56.2	0.39	0.001
marrubioides vs nuttallii	0.85	56.1	0.58	0.001
arcuatus vs densiflorus (SD & SA)	1.18	55.7	0.54	0.001
enigmaticus vs foliosus (coastal)	0.87	55.7	0.61	0.001
enigmaticus vs Vandenberg	0.85	55.7	0.64	0.001
howellii vs involucratus	1.06	55.6	0.50	0.001
abbottii vs involucratus	1.04	55.5	0.52	0.001
davidsonii (south) vs densiflorus (SD & SA)	1.25	55.3	0.53	0.001
aboriginum vs arcuatus	0.81	55.1	0.57	0.001
abbottii vs arcuatus	0.80	54.8	0.57	0.001
arcuatus vs enigmaticus	0.66	54.8	0.57	0.001
densiflorus (SJ) vs nesioticus	1.13	54.8	0.71	0.001
abbottii vs howellii	0.99	54.6	0.57	0.001
clementinus vs fasciculatus_ss	0.71	54.6	0.52	0.001
davidsonii (north) vs densiflorus (SD & SA)	1.25	54.5	0.55	0.001
nesioticus vs Shasta	0.63	54.3	0.72	0.001
fremontii (south) vs viscidus	0.97	54.3	0.61	0.001
fremontii (south) vs nuttallii	0.85	54.0	0.60	0.001
catalinensis vs Shasta	0.56	53.9	0.65	0.001
abbottii vs Shasta	0.88	53.9	0.66	0.001
densiflorus (SD & SA) vs nesioticus	1.27	53.8	0.59	0.001
foliosus (inland) vs nesioticus	1.05	53.3	0.66	0.001
densiflorus (SD & SA) vs gracilis	1.25	53.0	0.59	0.001
enigmaticus vs laxiflorus	0.54	52.7	0.41	0.001
foliosus (coastal) vs jonesii	0.87	52.7	0.59	0.001
helleri vs laxiflorus	0.74	52.6	0.41	0.001
hallii vs marrubioides	0.71	52.3	0.52	0.001
enigmaticus vs jonesii	0.60	51.9	0.56	0.001
catalinensis vs howellii	0.74	51.6	0.55	0.001
fasciculatus_ss vs niveus	0.64	51.5	0.48	0.001
arcuatus vs densiflorus (SJ)	1.13	51.5	0.62	0.001
davidsonii (north) vs jonesii	0.76	51.1	0.57	0.001
aboriginum vs catalinensis	0.60	50.7	0.57	0.001
fasciculatus_ss vs Shasta	0.55	50.5	0.56	0.001
clementinus vs enigmaticus	0.70	50.4	0.57	0.001
palmeri vs Shasta	0.83	50.3	0.61	0.001
niveus vs Shasta	0.83	50.3	0.60	0.001
abbottii vs densiflorus (SJ)	1.13	49.9	0.63	0.001
fremontii (north) vs hallii	0.60	49.9	0.59	0.001
fremontii (north) vs nuttallii	0.68	49.9	0.65	0.001
aboriginum vs palmeri	0.80	49.7	0.54	0.001
arcuatus vs nuttallii	0.60	49.4	0.53	0.001
howellii vs orbiculatus	0.82	49.4	0.39	0.001
nuttallii vs orbiculatus	0.85	49.4	0.40	0.001

pairs	SumsOfSqs	pseudo-F	R2	p-value
abbottii vs hallii	0.70	49.4	0.51	0.001
marrubioides vs viscidus	1.04	49.2	0.56	0.001
aboriginum vs howellii	0.93	49.0	0.54	0.001
arcuatus vs involucratus	0.84	48.9	0.47	0.001
fremontii (north) vs laxiflorus	0.58	48.8	0.44	0.001
catalinensis vs gracilis	0.68	48.7	0.61	0.001
jonesii vs laxiflorus	0.59	48.5	0.38	0.001
fremontii (south) vs jonesii	0.75	48.4	0.57	0.001
densiflorus (SJ) vs lucianus	0.84	48.3	0.61	0.001
enigmaticus vs niveus	0.70	48.0	0.52	0.001
abbottii vs fasciculatus/foliosus int.	0.95	48.0	0.56	0.001
foliosus (inland) vs viscidus	1.01	47.8	0.58	0.001
catalinensis vs clementinus	0.63	47.6	0.55	0.001
catalinensis vs involucratus	0.81	47.2	0.47	0.001
abbottii vs davidsonii (north)	0.83	47.2	0.56	0.001
jonesii vs orbiculatus	0.76	47.1	0.39	0.001
davidsonii (north) vs howellii	0.78	47.0	0.53	0.001
davidsonii (north) vs foliosus (inland)	0.96	46.6	0.58	0.001
enigmaticus vs gracilis	0.70	46.5	0.61	0.001
involucratus vs Vandenberg	0.90	46.5	0.51	0.001
aboriginum vs densiflorus (SD & SA)	1.08	46.5	0.51	0.001
aboriginum vs nesioticus	0.64	46.1	0.60	0.001
enigmaticus vs helleri	0.65	46.0	0.54	0.001
foliosus (inland) vs involucratus	0.87	46.0	0.48	0.001
densiflorus (SJ) vs gracilis	1.08	45.9	0.69	0.001
abbottii vs catalinensis	0.71	45.9	0.54	0.001
foliosus (inland) vs palmeri	0.78	45.8	0.54	0.001
densiflorus (SD & SA) vs involucratus	1.06	45.6	0.44	0.001
fremontii (south) vs gracilis	0.87	45.6	0.64	0.001
foliosus (inland) vs jonesii	0.85	45.5	0.55	0.001
fasciculatus_ss vs marrubioides	0.63	45.3	0.47	0.001
hallii vs orbiculatus	0.71	45.2	0.36	0.001
gracilis vs orbiculatus	0.81	45.2	0.41	0.001
davidsonii (north) vs niveus	0.73	45.2	0.51	0.001
enigmaticus vs howellii	0.72	45.1	0.52	0.001
catalinensis vs marrubioides	0.62	45.1	0.53	0.001
foliosus (coastal) vs marrubioides	0.84	45.1	0.56	0.001
catalinensis vs niveus	0.58	44.9	0.50	0.001
foliosus (coastal) vs helleri	0.82	44.8	0.55	0.001
davidsonii (north) vs enigmaticus	0.59	44.7	0.55	0.001
davidsonii (south) vs involucratus	0.82	44.6	0.44	0.001
fasciculatus/foliosus int. vs Vandenberg	0.93	44.4	0.60	0.001
fremontii (north) vs gracilis	0.85	44.4	0.72	0.001
aboriginum vs clementinus	0.72	44.3	0.54	0.001

pairs	SumsOfSqs	pseudo-F	R2	p-value
fasciculatus_ss vs gracilis	0.59	44.3	0.51	0.001
clementinus vs nesioticus	0.67	44.1	0.59	0.001
howellii vs niveus	0.72	44.1	0.48	0.001
foliosus (inland) vs orbiculatus	0.86	43.9	0.39	0.001
abbottii vs foliosus (coastal)	0.86	43.8	0.56	0.001
densiflorus (SD & SA) vs fasciculatus/foliosus int.	1.04	43.5	0.50	0.001
gracilis vs laxiflorus	0.59	43.4	0.39	0.001
helleri vs orbiculatus	0.86	43.3	0.37	0.001
orbiculatus vs Vandenberg	0.74	43.2	0.40	0.001
aboriginum vs Vandenberg	0.76	43.2	0.58	0.001
foliosus (inland) vs helleri	0.87	43.0	0.54	0.001
arcuatus vs nesioticus	0.49	42.6	0.56	0.001
niveus vs orbiculatus	0.77	42.6	0.35	0.001
marrubioides vs orbiculatus	0.72	42.6	0.37	0.001
aboriginum vs marrubioides	0.77	42.5	0.52	0.001
foliosus (coastal) vs howellii	0.86	42.5	0.52	0.001
davidsonii (south) vs Vandenberg	0.85	42.3	0.55	0.001
davidsonii (north) vs marrubioides	0.73	42.2	0.53	0.001
foliosus (coastal) vs involucratus	0.81	42.1	0.46	0.001
abbottii vs davidsonii (south)	0.86	42.0	0.50	0.001
densiflorus (SD & SA) vs howellii	1.10	42.0	0.46	0.001
involucratus vs marrubioides	0.74	41.8	0.44	0.001
enigmaticus vs fasciculatus/foliosus int.	0.61	41.8	0.53	0.001
"Baja East"/fasciculatus int. vs palmeri	0.71	41.8	0.59	0.001
foliosus (coastal) vs nesioticus	0.79	41.8	0.60	0.001
arcuatus vs Shasta	0.58	41.6	0.57	0.001
abbottii vs foliosus (inland)	0.85	41.3	0.54	0.001
densiflorus (SD & SA) vs fremontii (south)	1.01	41.3	0.50	0.001
fremontii (north) vs jonesii	0.56	41.2	0.60	0.001
clementinus vs densiflorus (SD & SA)	0.92	41.1	0.48	0.001
densiflorus (SJ) vs orbiculatus	0.75	41.0	0.39	0.001
helleri vs Shasta	0.70	41.0	0.59	0.001
jonesii vs marrubioides	0.63	41.0	0.50	0.001
densiflorus (SD & SA) vs foliosus (coastal)	0.99	40.9	0.49	0.001
mendocinensis vs palmeri	0.61	40.9	0.60	0.001
arcuatus vs gracilis	0.63	40.8	0.55	0.001
howellii vs nesioticus	0.68	40.7	0.54	0.001
davidsonii (north) vs densiflorus (SJ)	0.85	40.6	0.59	0.001
davidsonii (north) vs helleri	0.79	40.6	0.52	0.001
lucianus vs parishii	0.75	40.4	0.64	0.003
niveus vs nuttallii	0.53	40.4	0.47	0.001
fasciculatus/foliosus int. vs howellii	0.79	40.1	0.49	0.001
marrubioides vs Vandenberg	0.75	39.7	0.55	0.001
marrubioides vs nesioticus	0.62	39.4	0.55	0.001

pairs	SumsOfSqs	pseudo-F	R2	p-value
fremontii (south) vs marrubioides	0.70	39.3	0.53	0.001
clementinus vs foliosus (coastal)	0.70	39.2	0.53	0.001
arcuatus vs foliosus (coastal)	0.68	39.2	0.51	0.001
foliosus (coastal) vs orbiculatus	0.72	39.0	0.36	0.001
fremontii (north) vs palmeri	0.59	39.0	0.57	0.001
davidsonii (south) vs marrubioides	0.73	38.9	0.48	0.001
fasciculatus/foliosus int. vs involucratus	0.76	38.7	0.43	0.001
densiflorus (SD & SA) vs marrubioides	0.97	38.7	0.46	0.001
hallii vs niveus	0.48	38.4	0.42	0.001
abbottii vs fremontii (north)	0.69	38.1	0.60	0.001
mendocinensis vs Vandenberg	0.74	37.9	0.70	0.001
fremontii (south) vs niveus	0.72	37.9	0.49	0.001
arcuatus vs catalinensis	0.42	37.7	0.47	0.001
arcuatus vs davidsonii (north)	0.56	37.7	0.48	0.001
davidsonii (south) vs jonesii	0.69	37.6	0.46	0.001
abbottii vs jonesii	0.60	37.1	0.48	0.001
fasciculatus/foliosus int. vs marrubioides	0.73	37.1	0.49	0.001
clementinus vs involucratus	0.76	36.9	0.42	0.001
davidsonii (south) vs niveus	0.67	36.9	0.43	0.001
arcuatus vs howellii	0.63	36.6	0.45	0.001
catalinensis vs hallii	0.44	36.5	0.43	0.001
enigmaticus vs foliosus (inland)	0.69	36.5	0.51	0.001
foliosus (coastal) vs niveus	0.65	36.3	0.47	0.001
jonesii vs nuttallii	0.47	36.1	0.46	0.001
davidsonii (south) vs hallii	0.62	36.1	0.41	0.001
involucratus vs nesioticus	0.73	36.0	0.44	0.001
fremontii (south) vs involucratus	0.73	35.9	0.43	0.001
enigmaticus vs nesioticus	0.43	35.9	0.54	0.001
clementinus vs davidsonii (north)	0.60	35.8	0.49	0.001
densiflorus (SD & SA) vs enigmaticus	0.83	35.7	0.44	0.001
davidsonii (south) vs enigmaticus	0.57	35.6	0.46	0.001
clementinus vs foliosus (inland)	0.76	35.6	0.50	0.001
catalinensis vs jonesii	0.43	35.6	0.46	0.001
arcuatus vs clementinus	0.57	35.5	0.46	0.001
marrubioides vs niveus	0.60	35.4	0.44	0.001
densiflorus (SD & SA) vs Vandenberg	0.89	35.2	0.48	0.001
fasciculatus_ss vs helleri	0.52	35.2	0.41	0.001
jonesii vs nesioticus	0.41	35.2	0.52	0.001
gracilis vs marrubioides	0.65	35.0	0.53	0.001
aboriginum vs fasciculatus/foliosus int.	0.65	34.9	0.49	0.001
fasciculatus_ss vs fremontii (south)	0.48	34.9	0.43	0.001
helleri vs marrubioides	0.65	34.9	0.47	0.001
gracilis vs hallii	0.49	34.9	0.47	0.001
densiflorus (SD & SA) vs viscidus	0.90	34.9	0.44	0.001

pairs	SumsOfSqs	pseudo-F	R2	p-value
aboriginum vs orbiculatus	0.57	34.8	0.32	0.001
foliosus (coastal) vs Vandenberg	0.79	34.7	0.55	0.001
enigmaticus vs fremontii (south)	0.56	34.7	0.50	0.001
hallii vs laxiflorus	0.40	34.6	0.29	0.001
fasciculatus_ss vs nuttallii	0.41	34.4	0.40	0.001
davidsonii (north) vs nuttallii	0.54	34.4	0.47	0.001
densiflorus (SJ) vs foliosus (coastal)	0.85	34.3	0.57	0.001
arcuatus vs marrubioides	0.53	34.2	0.45	0.001
abbottii vs enigmaticus	0.56	34.2	0.47	0.001
nesioticus vs niveus	0.48	34.2	0.48	0.001
densiflorus (SJ) vs fasciculatus/foliosus int.	0.85	34.2	0.55	0.001
foliosus (inland) vs niveus	0.75	34.1	0.45	0.001
howellii vs Vandenberg	0.72	34.0	0.49	0.001
davidsonii (north) vs foliosus (coastal)	0.66	33.9	0.50	0.001
davidsonii (south) vs helleri	0.73	33.8	0.44	0.001
davidsonii (north) vs involucratus	0.64	33.7	0.40	0.001
densiflorus (SJ) vs involucratus	0.77	33.5	0.44	0.001
enigmaticus vs fasciculatus_ss	0.37	33.4	0.40	0.001
helleri vs howellii	0.59	33.3	0.44	0.001
davidsonii (south) vs foliosus (inland)	0.81	33.2	0.46	0.001
aboriginum vs foliosus (inland)	0.75	33.0	0.49	0.001
davidsonii (north) vs laxiflorus	0.43	32.9	0.30	0.001
aboriginum vs foliosus (coastal)	0.70	32.6	0.48	0.001
densiflorus (SD & SA) vs foliosus (inland)	0.86	32.4	0.44	0.001
aboriginum vs densiflorus (SJ)	0.79	32.3	0.53	0.001
fasciculatus/foliosus int. vs niveus	0.58	32.2	0.43	0.001
davidsonii (north) vs Shasta	0.45	32.0	0.54	0.001
davidsonii (north) vs gracilis	0.60	32.0	0.52	0.001
enigmaticus vs involucratus	0.56	31.9	0.38	0.001
"Baja East" vs palmeri	0.47	31.9	0.53	0.001
fremontii (north) vs nesioticus	0.47	31.9	0.64	0.001
enigmaticus vs orbiculatus	0.48	31.8	0.30	0.001
davidsonii (south) vs gracilis	0.65	31.8	0.48	0.001
densiflorus (SJ) vs enigmaticus	0.68	31.8	0.52	0.001
davidsonii (south) vs howellii	0.64	31.8	0.41	0.001
aboriginum vs davidsonii (north)	0.50	31.7	0.46	0.001
fasciculatus_ss vs fremontii (north)	0.39	31.6	0.46	0.001
catalinensis vs helleri	0.51	31.6	0.44	0.001
fasciculatus/foliosus int. vs foliosus (inland)	0.79	31.6	0.48	0.001
abbottii vs nuttallii	0.56	31.6	0.44	0.001
davidsonii (south) vs laxiflorus	0.47	31.5	0.28	0.001
arcuatus vs fasciculatus_ss	0.37	31.5	0.37	0.001
catalinensis vs fremontii (north)	0.40	31.5	0.55	0.001
clementinus vs howellii	0.59	31.3	0.43	0.001

pairs	SumsOfSqs	pseudo-F	R2	p-value
aboriginum vs fremontii (south)	0.61	31.2	0.48	0.001
fremontii (south) vs nesioticus	0.52	31.0	0.53	0.001
foliosus (coastal) vs fremontii	0.70	31.0	0.50	0.001
foliosus (coastal) vs gracilis	0.59	30.6	0.53	0.001
catalinensis vs fremontii (south)	0.46	30.6	0.47	0.001
hallii vs helleri	0.45	30.5	0.39	0.001
davidsonii (north) vs hallii	0.51	30.5	0.40	0.001
aboriginum vs davidsonii (south)	0.61	30.2	0.42	0.001
abbottii vs nesioticus	0.48	30.2	0.49	0.001
foliosus (inland) vs howellii	0.73	30.1	0.44	0.001
catalinensis vs davidsonii (north)	0.44	30.0	0.44	0.001
abbottii vs niveus	0.50	30.0	0.41	0.001
clementinus vs davidsonii (south)	0.60	29.7	0.41	0.001
abbottii vs helleri	0.55	29.7	0.43	0.001
howellii vs marrubioides	0.57	29.6	0.41	0.001
helleri vs nuttallii	0.54	29.6	0.42	0.001
arcuatus vs foliosus (inland)	0.64	29.5	0.44	0.001
hallii vs nuttallii	0.35	29.4	0.37	0.001
foliosus (inland) vs gracilis	0.67	29.3	0.52	0.001
davidsonii (south) vs densiflorus (SJ)	0.80	29.3	0.47	0.001
"Baja East" vs Vandenberg	0.64	28.9	0.63	0.001
fremontii (north) vs viscidus	0.71	28.9	0.54	0.001
catalinensis vs enigmaticus	0.35	28.9	0.43	0.001
involucratus vs palmeri	0.59	28.8	0.34	0.001
arcuatus vs davidsonii (south)	0.56	28.6	0.39	0.001
gracilis vs nesioticus	0.44	28.4	0.55	0.001
marrubioides vs Shasta	0.55	28.4	0.49	0.001
clementinus vs Shasta	0.50	28.3	0.50	0.001
aboriginum vs enigmaticus	0.45	28.3	0.43	0.001
"Baja East"/fasciculatus int. vs Vandenberg	0.66	28.3	0.61	0.001
clementinus vs fasciculatus/foliosus int.	0.56	28.2	0.43	0.001
Shasta vs viscidus	0.66	28.2	0.50	0.001
fasciculatus_ss vs orbiculatus	0.42	27.9	0.25	0.001
mendocinensis vs viscidus	0.66	27.8	0.55	0.001
catalinensis vs orbiculatus	0.44	27.3	0.27	0.001
helleri vs nesioticus	0.47	27.1	0.46	0.001
arcuatus vs hallii	0.30	27.1	0.35	0.001
fasciculatus/foliosus int. vs Shasta	0.50	26.9	0.50	0.001
fasciculatus/foliosus int. vs nuttallii	0.50	26.9	0.41	0.001
nesioticus vs orbiculatus	0.47	26.8	0.29	0.001
fasciculatus/foliosus int. vs laxiflorus	0.39	26.7	0.26	0.001
enigmaticus vs Shasta	0.40	26.7	0.49	0.001
foliosus (inland) vs fremontii (south)	0.75	26.7	0.46	0.001
arcuatus vs niveus	0.43	26.6	0.36	0.001

pairs	SumsOfSqs	pseudo-F	R2	p-value
enigmaticus vs marrubioides	0.44	26.6	0.41	0.001
gracilis vs helleri	0.49	26.5	0.46	0.001
arcuatus vs orbiculatus	0.45	26.2	0.26	0.001
fasciculatus/foliosus int. vs gracilis	0.56	25.9	0.47	0.001
fasciculatus/foliosus int. vs helleri	0.56	25.9	0.40	0.001
davidsonii (north) vs fremontii (north)	0.46	25.7	0.52	0.001
davidsonii (south) vs nuttallii	0.53	25.7	0.37	0.001
mendocinensis vs Shasta	0.40	25.6	0.66	0.001
clementinus vs densiflorus (SJ)	0.62	25.5	0.47	0.001
"Baja East" vs viscidus	0.66	25.5	0.52	0.001
lucianus vs viscidus	0.54	25.4	0.39	0.001
Shasta vs Vandenberg	0.56	25.4	0.55	0.001
catalinensis vs nuttallii	0.31	25.2	0.38	0.001
davidsonii (north) vs fasciculatus_ss	0.38	25.2	0.34	0.001
clementinus vs orbiculatus	0.43	25.1	0.26	0.001
hallii vs nesioticus	0.33	25.1	0.39	0.001
davidsonii (south) vs Shasta	0.52	25.1	0.44	0.001
foliosus (inland) vs marrubioides	0.55	25.0	0.41	0.001
davidsonii (north) vs fremontii (south)	0.47	25.0	0.43	0.001
"Baja East"/fasciculatus int. vs nuttallii	0.44	24.9	0.48	0.001
fremontii (south) vs Vandenberg	0.53	24.9	0.48	0.001
parishii vs Vandenberg	0.58	24.7	0.64	0.003
gracilis vs nuttallii	0.40	24.7	0.44	0.001
fasciculatus_ss vs jonesii	0.32	24.7	0.32	0.001
clementinus vs Vandenberg	0.46	24.6	0.44	0.001
"Baja East"/fasciculatus int. vs laxiflorus	0.33	24.5	0.28	0.001
"Baja East"/fasciculatus int. vs howellii	0.55	24.4	0.46	0.001
howellii vs Shasta	0.49	24.0	0.43	0.001
"Baja East"/fasciculatus int. vs viscidus	0.65	23.8	0.49	0.001
fasciculatus_ss vs hallii	0.30	23.8	0.29	0.001
gracilis vs niveus	0.40	23.6	0.40	0.001
foliosus (coastal) vs mendocinensis	0.54	23.5	0.54	0.001
foliosus (inland) vs mendocinensis	0.60	23.4	0.54	0.001
densiflorus (SJ) vs fremontii (south)	0.65	23.3	0.48	0.001
enigmaticus vs fremontii (north)	0.37	23.3	0.48	0.001
densiflorus (SJ) vs viscidus	0.58	23.0	0.44	0.001
fremontii (south) vs helleri	0.48	22.9	0.40	0.001
hallii vs jonesii	0.30	22.9	0.32	0.001
palmeri vs parishii	0.39	22.8	0.48	0.001
densiflorus (SJ) vs marrubioides	0.58	22.7	0.43	0.001
fasciculatus/foliosus int. vs foliosus (coastal)	0.53	22.7	0.40	0.001
jonesii vs niveus	0.34	22.6	0.33	0.001
catalinensis vs laxiflorus	0.24	22.6	0.23	0.001
howellii vs mendocinensis	0.43	22.5	0.45	0.001

pairs	SumsOfSqs	pseudo-F	R2	p-value
lucianus vs santa_rosa	0.43	22.3	0.50	0.009
davidsonii (south) vs foliosus (coastal)	0.51	22.3	0.36	0.001
fremontii (north) vs mendocinensis	0.40	22.1	0.69	0.001
densiflorus (SD & SA) vs mendocinensis	0.66	22.0	0.42	0.001
abbottii vs "Baja East"/fasciculatus int.	0.49	21.9	0.47	0.001
arcuatus vs helleri	0.34	21.8	0.34	0.001
fasciculatus/foliosus int. vs jonesii	0.39	21.8	0.36	0.001
arcuatus vs fremontii (south)	0.43	21.7	0.37	0.001
aboriginum vs mendocinensis	0.37	21.7	0.49	0.001
fasciculatus/foliosus int. vs fremontii (north)	0.48	21.5	0.47	0.001
fasciculatus/foliosus int. vs fremontii (south)	0.49	21.4	0.39	0.001
orbiculatus vs Shasta	0.37	21.4	0.25	0.001
foliosus (inland) vs Vandenberg	0.54	21.4	0.43	0.001
densiflorus (SJ) vs howellii	0.61	21.3	0.39	0.001
fasciculatus/foliosus int. vs orbiculatus	0.42	21.1	0.23	0.001
abbottii vs marrubioides	0.43	21.0	0.35	0.001
arcuatus vs mendocinensis	0.27	20.8	0.44	0.001
densiflorus (SJ) vs mendocinensis	0.64	20.7	0.60	0.001
arcuatus vs jonesii	0.29	20.7	0.33	0.001
aboriginum vs "Baja East"/fasciculatus int.	0.41	20.7	0.45	0.001
foliosus (coastal) vs fremontii (north)	0.52	20.6	0.48	0.001
foliosus (inland) vs Shasta	0.55	20.4	0.45	0.001
clementinus vs mendocinensis	0.39	20.3	0.47	0.001
aboriginum vs fremontii (north)	0.44	20.2	0.45	0.001
fasciculatus_ss vs laxiflorus	0.22	20.2	0.19	0.001
densiflorus (SJ) vs foliosus (inland)	0.65	20.1	0.44	0.001
"Baja East" vs howellii	0.42	19.9	0.42	0.001
densiflorus (SJ) vs Vandenberg	0.52	19.9	0.47	0.001
davidsonii (south) vs fasciculatus_ss	0.37	19.8	0.27	0.001
parishii vs viscidus	0.52	19.8	0.48	0.002
densiflorus (SD & SA) vs Shasta	0.58	19.7	0.36	0.001
foliosus (coastal) vs Shasta	0.47	19.7	0.44	0.001
catalinensis vs fasciculatus/foliosus int.	0.32	19.4	0.34	0.001
"Baja East" vs clementinus	0.37	19.2	0.44	0.001
fremontii (north) vs involucratus	0.45	19.2	0.33	0.001
"Baja East"/fasciculatus int. vs nesioticus	0.35	19.2	0.52	0.001
parishii vs Shasta	0.35	19.1	0.63	0.003
mendocinensis vs niveus	0.31	18.8	0.39	0.001
clementinus vs parishii	0.38	18.7	0.47	0.003
fremontii (north) vs Vandenberg	0.46	18.4	0.51	0.001
fremontii (north) vs niveus	0.39	18.4	0.37	0.001
densiflorus (SJ) vs Shasta	0.51	18.3	0.49	0.001
davidsonii (south) vs fremontii (south)	0.41	18.3	0.33	0.001
arcuatus vs fasciculatus/foliosus int.	0.33	18.2	0.31	0.001

pairs	SumsOfSqs	pseudo-F	R2	p-value
involucratus vs Shasta	0.42	18.1	0.30	0.001
fremontii (north) vs marrubioides	0.37	18.1	0.41	0.001
palmeri vs santa_rosa	0.29	18.0	0.43	0.007
davidsonii (north) vs nesioticus	0.31	17.8	0.37	0.001
aboriginum vs involucratus	0.36	17.7	0.25	0.001
gracilis vs jonesii	0.31	17.6	0.35	0.001
"Baja East"/fasciculatus int. vs clementinus	0.38	17.5	0.41	0.001
helleri vs jonesii	0.28	17.5	0.30	0.001
densiflorus (SD & SA) vs fremontii (north)	0.55	17.4	0.35	0.001
"Baja East" vs nuttallii	0.27	17.3	0.40	0.001
fremontii (south) vs Shasta	0.36	17.3	0.42	0.001
arcuatus vs fremontii (north)	0.31	17.2	0.38	0.001
"Baja East"/fasciculatus int. vs gracilis	0.40	17.2	0.50	0.001
jonesii vs mendocinensis	0.26	17.1	0.41	0.001
mendocinensis vs parishii	0.20	16.7	0.74	**0.019**
catalinensis vs davidsonii (south)	0.32	16.7	0.28	0.001
Vandenberg vs viscidus	0.42	16.7	0.35	0.001
davidsonii (south) vs orbiculatus	0.32	16.6	0.18	0.001
"Baja East" vs Shasta	0.35	16.4	0.54	0.001
fasciculatus/foliosus int. vs nesioticus	0.31	16.4	0.35	0.001
abbottii vs gracilis	0.34	16.3	0.35	0.001
fremontii (south) vs orbiculatus	0.30	16.2	0.19	0.001
helleri vs niveus	0.28	16.1	0.26	0.001
"Baja East"/fasciculatus int. vs marrubioides	0.39	16.0	0.38	0.001
enigmaticus vs mendocinensis	0.23	16.0	0.41	0.001
densiflorus (SJ) vs parishii	0.57	16.0	0.57	0.002
fremontii (north) vs orbiculatus	0.32	15.9	0.21	0.001
fremontii (north) vs helleri	0.32	15.8	0.38	0.001
fasciculatus/foliosus int. vs hallii	0.25	15.7	0.25	0.001
densiflorus (SJ) vs fremontii (north)	0.55	15.6	0.49	0.001
"Baja East" vs densiflorus (SJ)	0.57	15.5	0.51	0.001
clementinus vs fremontii (north)	0.33	15.5	0.38	0.001
"Baja East" vs foliosus (coastal)	0.39	15.4	0.42	0.001
"Baja East"/fasciculatus int. vs densiflorus (SJ)	0.54	15.4	0.49	0.001
aboriginum vs parishii	0.31	15.3	0.42	0.001
aboriginum vs Shasta	0.29	15.1	0.35	0.001
"Baja East"/fasciculatus int. vs hallii	0.27	15.1	0.31	0.001
foliosus (inland) vs fremontii (north)	0.47	15.0	0.41	0.001
"Baja East" vs densiflorus (SD & SA)	0.47	14.9	0.33	0.001
involucratus vs mendocinensis	0.35	14.9	0.29	0.001
"Baja East"/fasciculatus int. vs enigmaticus	0.27	14.7	0.37	0.001
fasciculatus_ss vs nesioticus	0.19	14.5	0.25	0.001
abbottii vs mendocinensis	0.31	14.2	0.38	0.001
"Baja East"/fasciculatus int. vs foliosus (inland)	0.41	14.1	0.39	0.001

pairs	SumsOfSqs	pseudo-F	R2	p-value
"Baja East" vs gracilis	0.34	14.1	0.47	0.001
davidsonii (south) vs fremontii (north)	0.36	14.1	0.33	0.001
"Baja East"/fasciculatus int. vs foliosus (coastal)	0.37	14.0	0.39	0.001
gracilis vs mendocinensis	0.29	14.0	0.48	0.002
"Baja East"/fasciculatus int. vs involucratus	0.35	14.0	0.26	0.001
"Baja East"/fasciculatus int. vs davidsonii (north)	0.33	13.9	0.37	0.001
fremontii (south) vs mendocinensis	0.33	13.9	0.42	0.002
"Baja East" vs foliosus (inland)	0.39	13.9	0.40	0.001
"Baja East"/fasciculatus int. vs fremontii (north)	0.40	13.8	0.53	0.003
"Baja East"/fasciculatus int. vs catalinensis	0.25	13.8	0.35	0.001
marrubioides vs mendocinensis	0.30	13.7	0.36	0.001
"Baja East"/fasciculatus int. vs jonesii	0.26	13.7	0.34	0.001
fremontii (north) vs Shasta	0.31	13.6	0.48	0.002
davidsonii (north) vs fasciculatus/foliosus int.	0.30	13.6	0.27	0.001
densiflorus (SD & SA) vs parishii	0.44	13.3	0.32	0.001
"Baja East"/fasciculatus int. vs niveus	0.27	13.2	0.30	0.001
helleri vs mendocinensis	0.29	13.2	0.35	0.001
"Baja East"/fasciculatus int. vs fremontii (south)	0.35	13.2	0.39	0.001
"Baja East" vs hallii	0.19	12.9	0.28	0.001
"Baja East" vs nesioticus	0.19	12.9	0.43	0.001
aboriginum vs "Baja East"	0.25	12.6	0.34	0.001
arcuatus vs "Baja East"	0.20	12.6	0.32	0.001
santa_rosa vs Vandenberg	0.32	12.5	0.49	**0.015**
"Baja East" vs involucratus	0.28	12.4	0.25	0.001
catalinensis vs mendocinensis	0.17	12.4	0.34	0.001
"Baja East" vs fremontii (south)	0.30	12.3	0.38	0.001
howellii vs parishii	0.27	12.3	0.33	0.002
"Baja East" vs davidsonii (north)	0.25	12.1	0.35	0.001
davidsonii (north) vs orbiculatus	0.22	12.1	0.14	0.001
enigmaticus vs parishii	0.20	12.1	0.37	0.002
"Baja East"/fasciculatus int. vs densiflorus (SD & SA)	0.40	12.1	0.27	0.001
laxiflorus vs nuttallii	0.17	12.0	0.13	0.001
arcuatus vs parishii	0.18	11.9	0.33	0.001
fremontii (north) vs parishii	0.30	11.9	0.60	0.008
davidsonii (south) vs nesioticus	0.26	11.9	0.25	0.001
"Baja East" vs fremontii (north)	0.30	11.8	0.52	0.001
fremontii (south) vs parishii	0.29	11.6	0.41	0.003
"Baja East" vs niveus	0.22	11.4	0.28	0.001
"Baja East" vs laxiflorus	0.15	11.4	0.16	0.001
"Baja East" vs jonesii	0.19	11.3	0.30	0.001
nesioticus vs nuttallii	0.16	11.3	0.26	0.001
jonesii vs parishii	0.17	11.2	0.33	0.004
"Baja East"/fasciculatus int. vs Shasta	0.28	11.2	0.43	0.001
"Baja East"/fasciculatus int. vs davidsonii (south)	0.31	11.0	0.28	0.001

pairs	SumsOfSqs	pseudo-F	R2	p-value
marrubioides vs parishii	0.25	10.9	0.33	0.003
jonesii vs santa_rosa	0.17	10.8	0.33	0.006
"Baja East"/fasciculatus int. vs mendocinensis	0.29	10.8	0.52	0.002
catalinensis vs parishii	0.16	10.7	0.33	0.001
foliosus (coastal) vs parishii	0.29	10.6	0.37	0.002
"Baja East"/fasciculatus int. vs helleri	0.27	10.6	0.29	0.001
clementinus vs fremontii (south)	0.23	10.6	0.24	0.001
abbottii vs "Baja East"	0.26	10.5	0.30	0.001
involucratus vs parishii	0.27	10.5	0.23	0.001
arcuatus vs "Baja East"/fasciculatus int.	0.20	10.5	0.27	0.001
davidsonii (south) vs fasciculatus/foliosus int.	0.29	10.4	0.20	0.001
foliosus (inland) vs parishii	0.33	10.3	0.36	0.001
fremontii (south) vs howellii	0.22	10.3	0.21	0.001
fasciculatus_ss vs parishii	0.15	10.3	0.24	0.001
"Baja East" vs marrubioides	0.24	10.3	0.29	0.001
hallii vs parishii	0.14	10.2	0.25	0.001
catalinensis vs fasciculatus_ss	0.13	10.0	0.16	0.001
fasciculatus/foliosus int. vs fasciculatus_ss	0.17	9.9	0.17	0.001
foliosus (coastal) vs foliosus (inland)	0.28	9.9	0.24	0.001
orbiculatus vs parishii	0.20	9.8	0.15	0.001
"Baja East" vs helleri	0.21	9.8	0.28	0.001
"Baja East"/fasciculatus int. vs orbiculatus	0.20	9.8	0.14	0.001
arcuatus vs santa_rosa	0.15	9.5	0.29	0.003
clementinus vs santa_rosa	0.21	9.3	0.32	0.005
fasciculatus/foliosus int. vs parishii	0.24	9.3	0.32	0.003
mendocinensis vs nesioticus	0.12	9.3	0.37	0.001
"Baja East"/fasciculatus int. vs fasciculatus_ss	0.16	9.1	0.20	0.001
"Baja East" vs mendocinensis	0.19	9.1	0.50	0.002
"Baja East" vs catalinensis	0.14	9.1	0.27	0.001
hallii vs santa_rosa	0.13	9.0	0.24	0.004
santa_rosa vs viscidus	0.25	8.9	0.31	0.004
"Baja East" vs davidsonii (south)	0.24	8.8	0.24	0.001
fasciculatus/foliosus int. vs mendocinensis	0.21	8.5	0.28	0.001
densiflorus (SD & SA) vs densiflorus (SJ)	0.30	8.5	0.19	0.001
fasciculatus_ss vs mendocinensis	0.12	8.5	0.20	0.001
"Baja East" vs fasciculatus/foliosus int.	0.21	8.5	0.27	0.001
fremontii (north) vs santa_rosa	0.22	8.4	0.55	**0.032**
hallii vs mendocinensis	0.14	8.4	0.21	0.001
mendocinensis vs orbiculatus	0.16	8.3	0.12	0.001
mendocinensis vs santa_rosa	0.11	8.2	0.62	**0.038**
davidsonii (north) vs mendocinensis	0.19	8.0	0.27	0.001
davidsonii (north) vs parishii	0.18	8.0	0.29	0.001
santa_rosa vs Shasta	0.16	7.8	0.44	**0.018**
laxiflorus vs nesioticus	0.10	7.8	0.10	0.001

pairs	SumsOfSqs	pseudo-F	R2	p-value
"Baja East" vs orbiculatus	0.16	7.7	0.12	0.001
"Baja East"/fasciculatus int. vs parishii	0.22	7.5	0.48	**0.010**
nuttallii vs santa_rosa	0.13	7.4	0.25	0.004
gracilis vs santa_rosa	0.18	7.3	0.38	**0.013**
howellii vs santa_rosa	0.17	7.3	0.23	0.004
foliosus (inland) vs santa_rosa	0.24	7.2	0.30	**0.011**
aboriginum vs santa_rosa	0.15	7.2	0.27	0.003
nesioticus vs parishii	0.12	7.2	0.34	0.001
davidsonii (south) vs mendocinensis	0.20	7.1	0.21	0.001
davidsonii (south) vs parishii	0.21	7.1	0.22	0.001
helleri vs parishii	0.16	6.9	0.24	0.002
catalinensis vs nesioticus	0.10	6.9	0.18	0.001
niveus vs parishii	0.13	6.8	0.20	0.001
densiflorus (SD & SA) vs santa_rosa	0.24	6.8	0.20	0.003
"Baja East" vs fasciculatus_ss	0.10	6.7	0.16	0.001
nuttallii vs parishii	0.13	6.7	0.23	0.001
foliosus (coastal) vs santa_rosa	0.20	6.7	0.28	0.006
niveus vs santa_rosa	0.13	6.4	0.20	0.003
densiflorus (SJ) vs santa_rosa	0.26	6.3	0.37	**0.018**
helleri vs santa_rosa	0.15	6.2	0.23	**0.011**
davidsonii (north) vs davidsonii (south)	0.14	6.0	0.13	0.001
marrubioides vs santa_rosa	0.14	5.9	0.22	0.005
fremontii (south) vs santa_rosa	0.15	5.8	0.27	**0.010**
involucratus vs santa_rosa	0.15	5.7	0.14	0.005
gracilis vs parishii	0.13	5.6	0.30	0.003
nesioticus vs santa_rosa	0.09	5.6	0.30	0.007
"Baja East" vs parishii	0.15	5.5	0.44	**0.013**
laxiflorus vs parishii	0.08	5.2	0.08	0.001
"Baja East"/fasciculatus int. vs fasciculatus/foliosus int.	0.13	5.2	0.18	0.001
fasciculatus/foliosus int. vs santa_rosa	0.14	5.0	0.21	0.005
abbottii vs parishii	0.12	4.7	0.18	0.001
abbottii vs santa_rosa	0.12	4.6	0.19	0.007
mendocinensis vs nuttallii	0.08	4.5	0.15	0.001
catalinensis vs santa_rosa	0.07	4.5	0.18	0.007
fremontii (south) vs fremontii (north)	0.13	4.5	0.18	0.001
"Baja East" vs enigmaticus	0.08	4.2	0.15	0.001
fasciculatus_ss vs santa_rosa	0.06	4.0	0.11	0.001
laxiflorus vs santa_rosa	0.06	4.0	0.06	0.002
parishii vs santa_rosa	0.10	4.0	0.57	**0.100**
davidsonii (north) vs santa_rosa	0.09	3.8	0.17	0.005
fremontii (north) vs howellii	0.10	3.8	0.12	0.001
"Baja East"/fasciculatus int. vs santa_rosa	0.13	3.6	0.34	**0.023**
enigmaticus vs santa_rosa	0.06	3.6	0.15	0.005

pairs	SumsOfSqs	pseudo-F	R2	p-value
"Baja East" vs "Baja East"/fasciculatus int.	0.11	3.2	0.23	0.003
laxiflorus vs mendocinensis	0.05	3.1	0.05	0.005
orbiculatus vs santa_rosa	0.06	2.6	0.05	**0.022**
davidsonii (south) vs santa_rosa	0.08	2.6	0.10	**0.012**
"Baja East" vs santa_rosa	0.06	1.8	0.23	**0.117**

Appendix 4 - Supplemental Figures

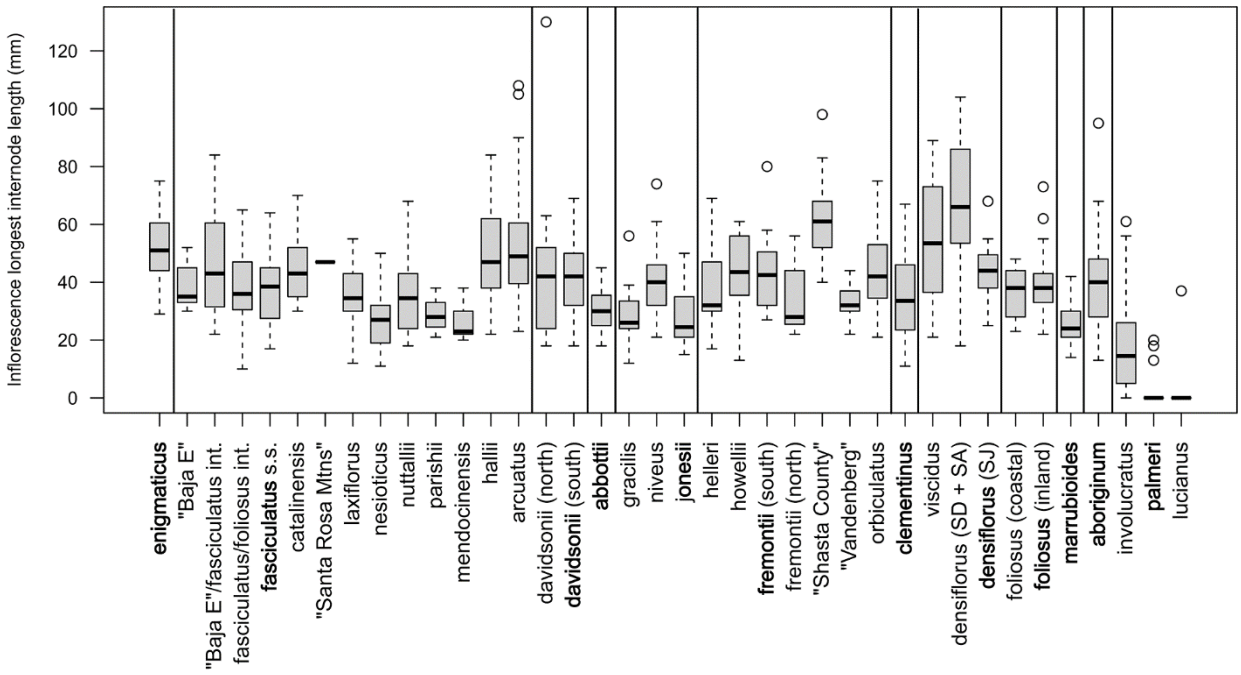

Figure S1. Boxplots comparing longest inflorescence internode length (mm) between final morphological groupings. Vertical lines divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

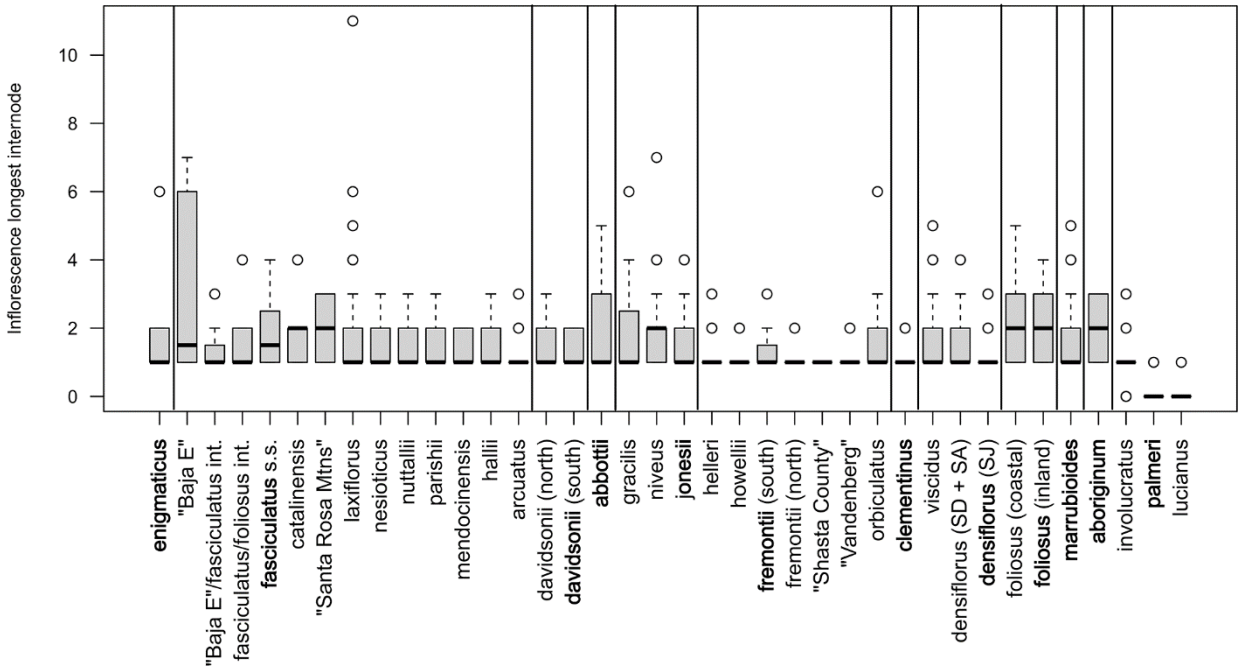

Figure S2. Boxplots comparing longest inflorescence internode position between final morphological groupings. Vertical lines divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

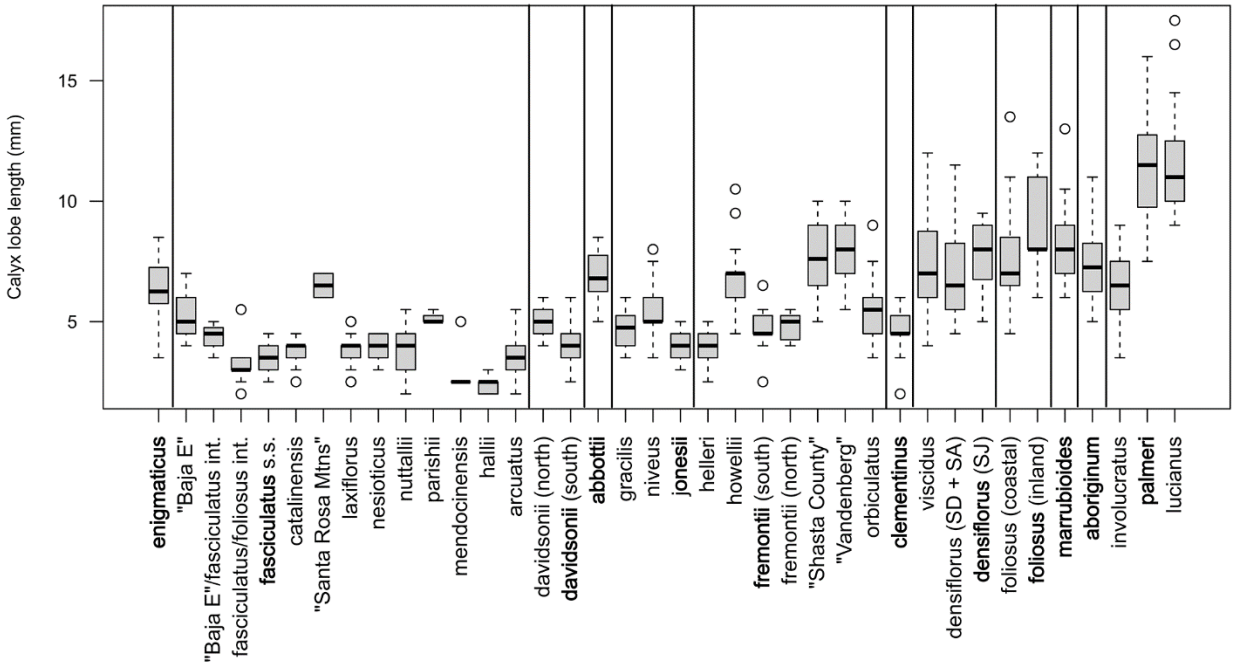

Figure S3. Boxplots comparing calyx lobe length between final morphological groupings. Vertical lines divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

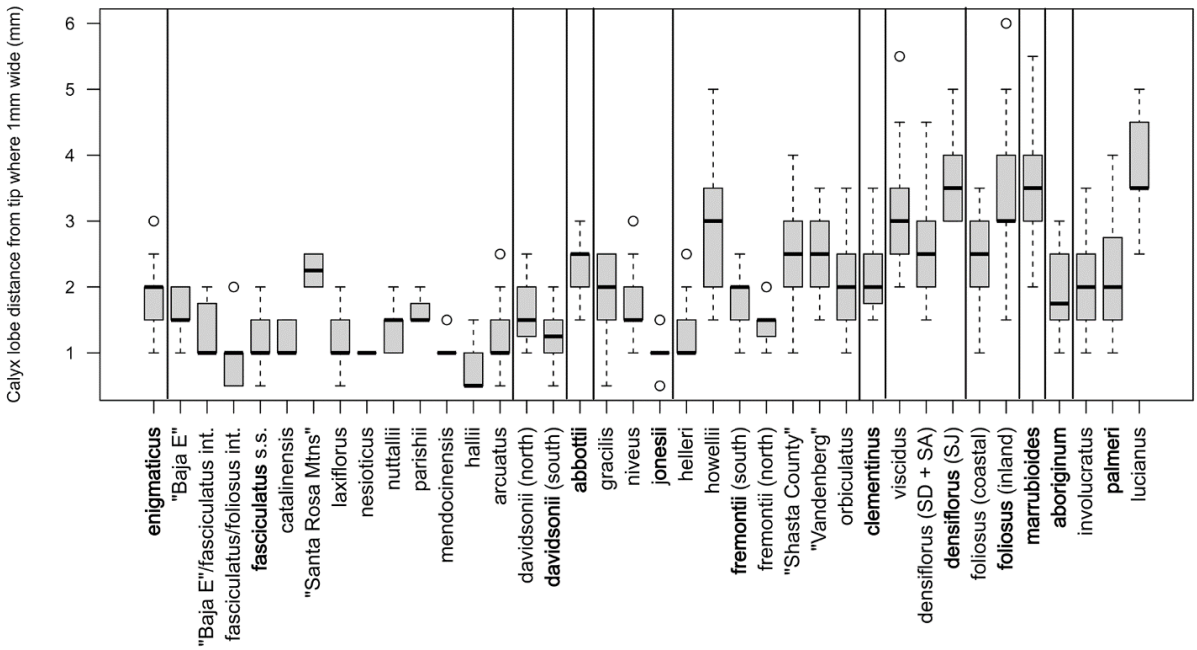

Figure S4. Boxplots comparing distance from the distal end of the calyx lobe to where it is 1 mm wide for final morphological groupings. Vertical lines divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

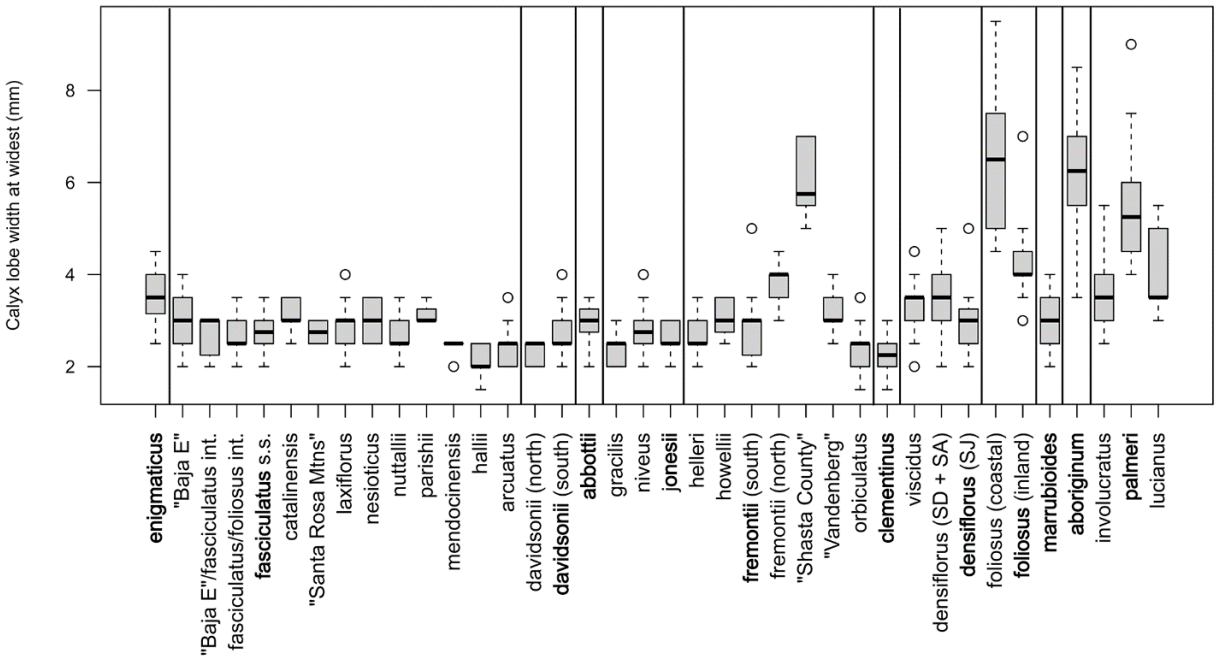

Figure S5. Boxplots comparing calyx lobe width at widest between final morphological groupings. Vertical lines divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

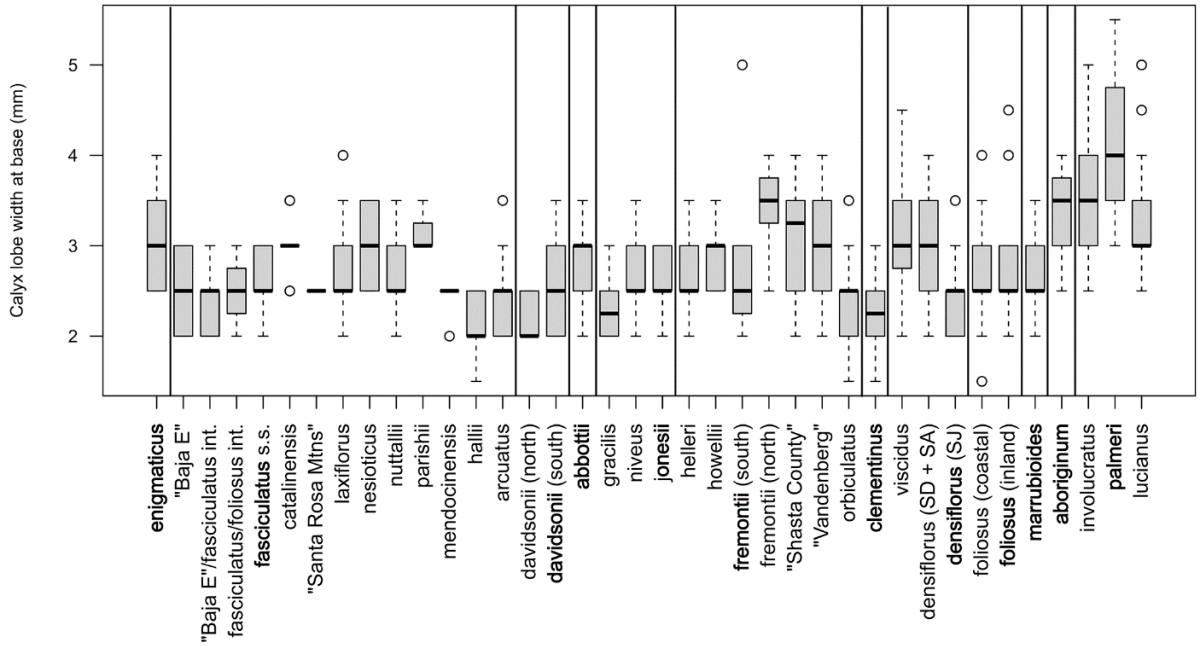

Figure S6. Boxplots comparing calyx lobe width at base between final morphological groupings. Vertical lines divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

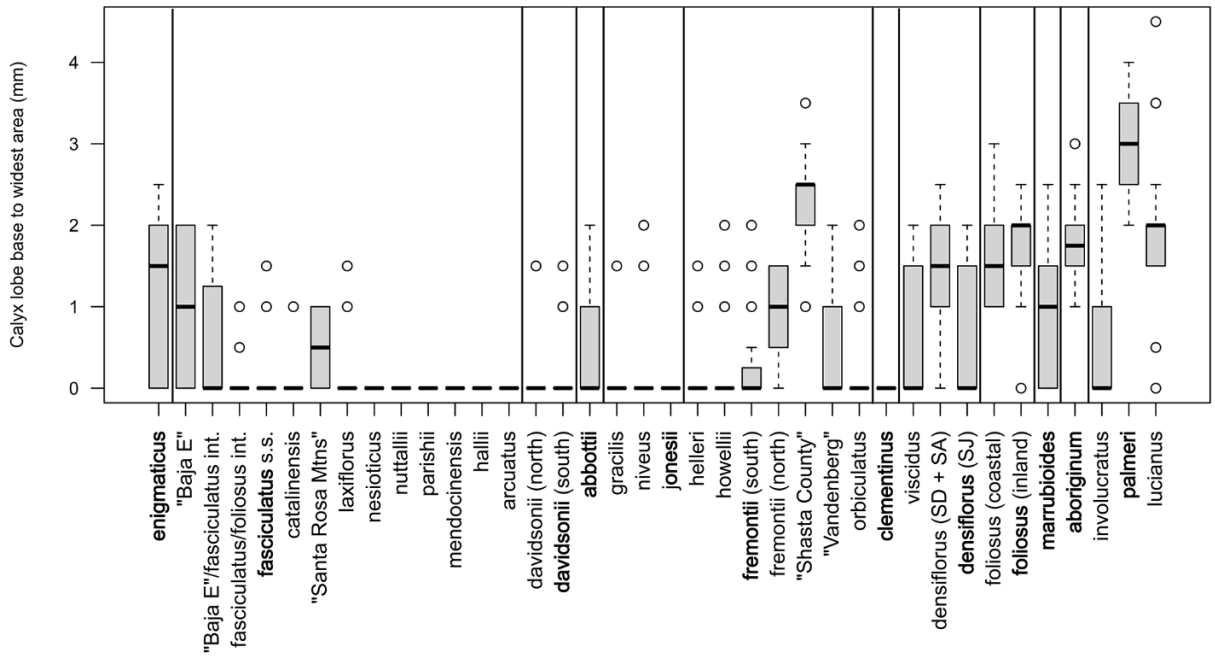

Figure S7. Boxplots comparing distance from calyx lobe base to widest area for final morphological groupings. Vertical lines divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

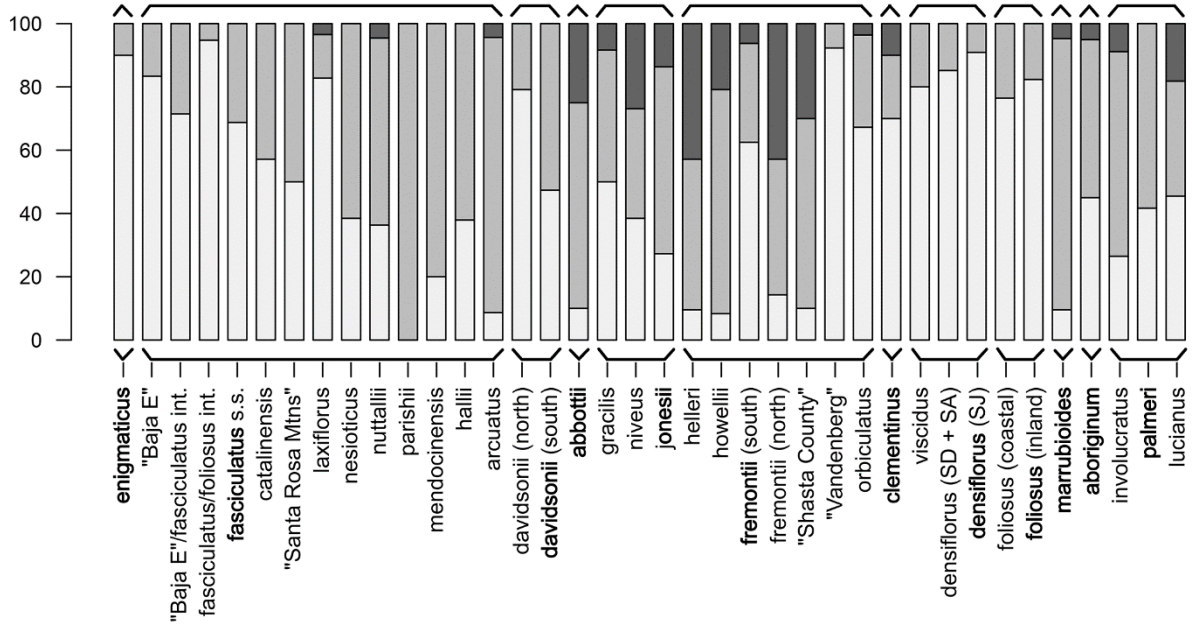

FIGURE S8. Stacked barplots showing the proportion of specimens with ridgelike calyx veins within final morphological groupings. Ridges on calyx veins: no ridge (pale grey), slightly protruding (medium grey), obviously protruding (dark grey). Brackets divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

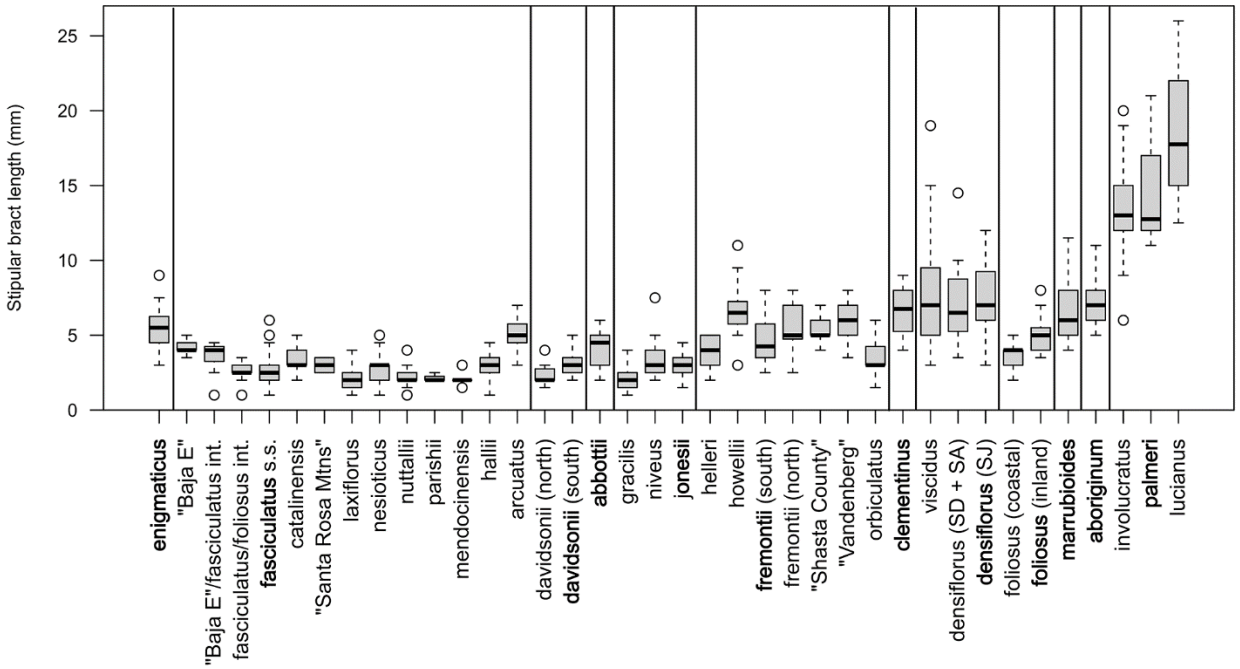

Figure S9. Boxplots comparing stipular bract length between final morphological groupings. Vertical lines divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

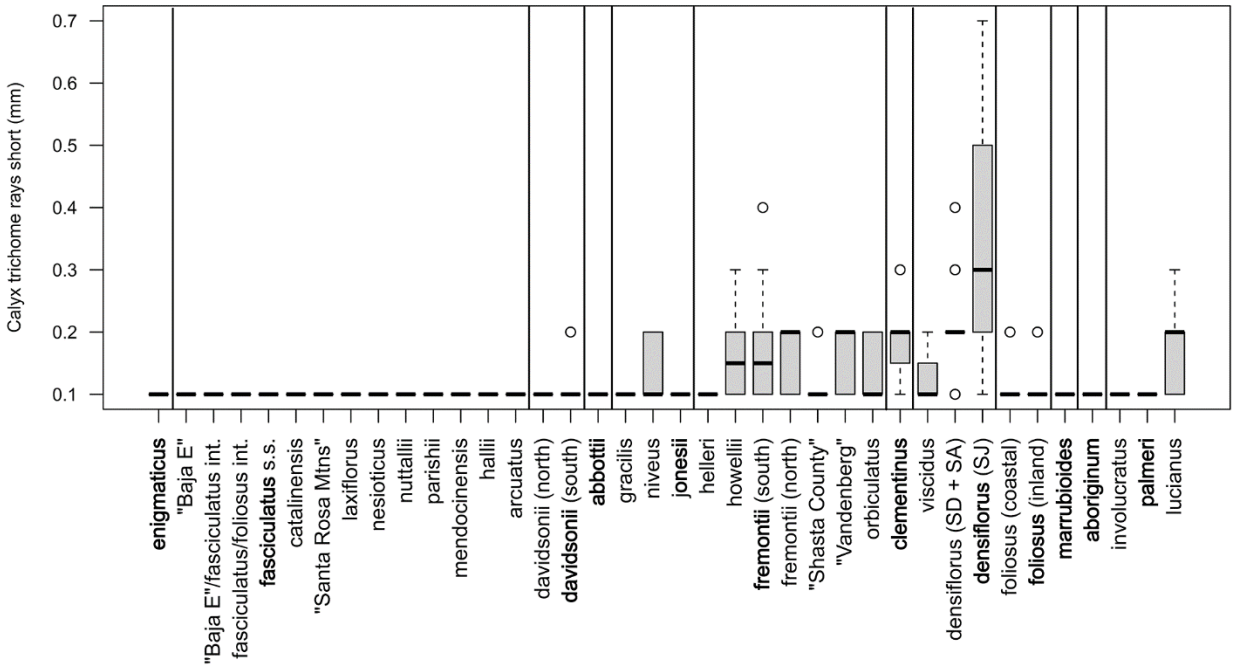

Figure S10. Boxplots comparing shortest stellate trichome rays on the calyx between final morphological groupings. Vertical lines divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

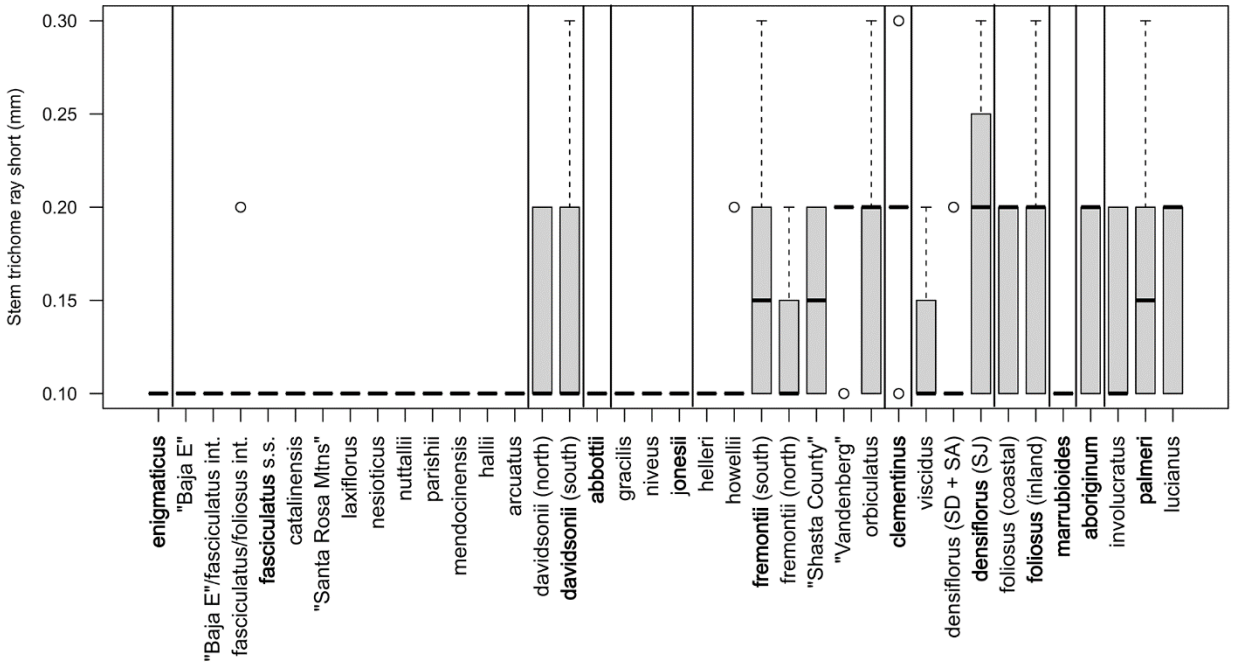

Figure S11. Boxplots comparing shortest stellate trichome rays on the stem between final morphological groupings. Vertical lines divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

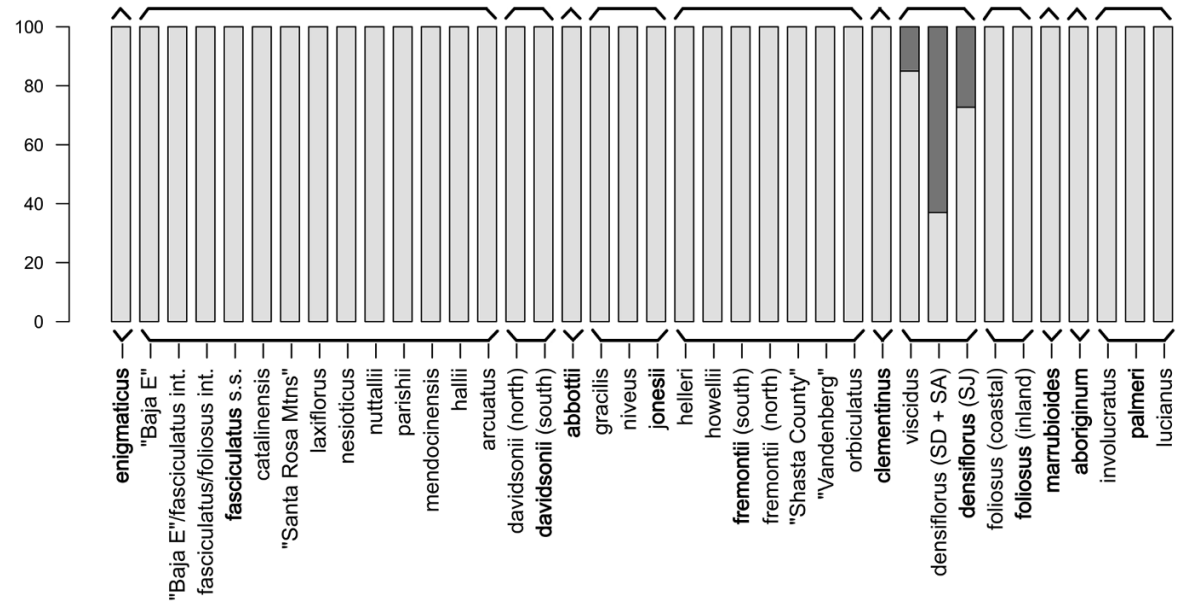

Figure S12. Stacked barplots showing the proportion of specimens with simple or bifurcate nonglandular trichomes on the abaxial side of the calyx within final morphological groupings. Absent (light grey), present (dark grey). Brackets divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

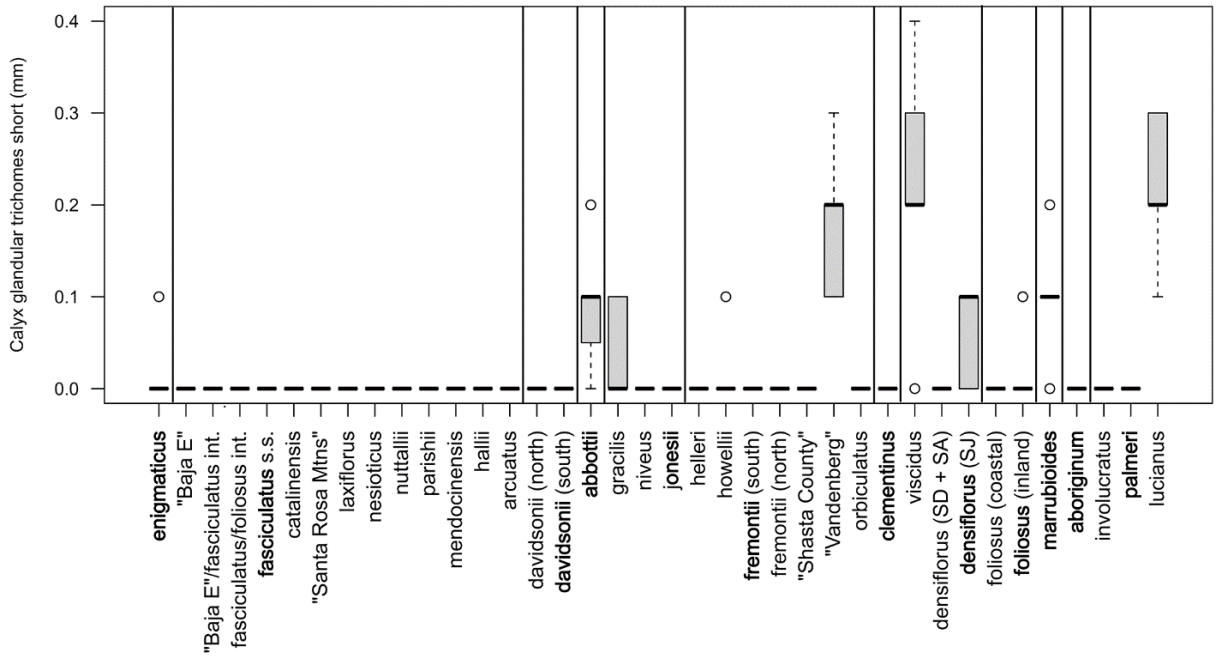

Figure S13. Boxplots comparing shortest glandular trichomes on the calyx between final morphological groupings. Vertical lines divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.

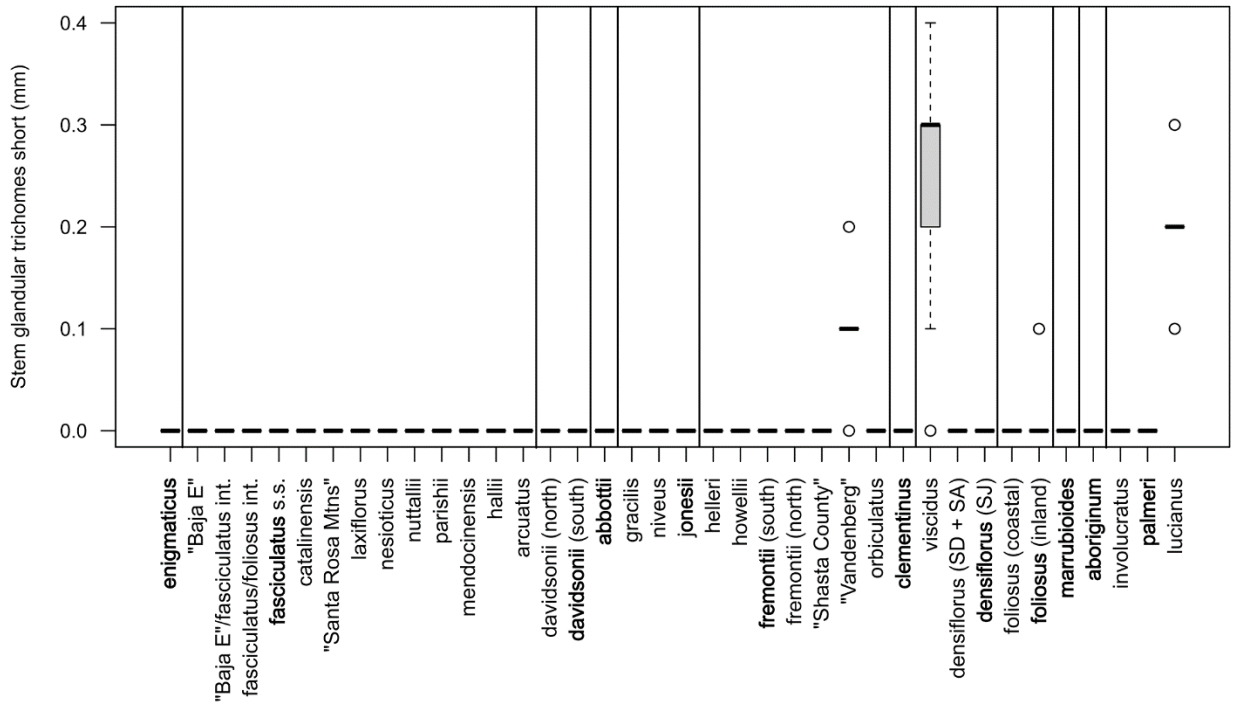

Figure S14. Boxplots comparing shortest glandular trichomes on the stem between final morphological groupings. Vertical lines divide morphological groupings into the species as recognized by Bates plus the more recently described *M. enigmaticus*. These 12 broader groups are labeled by bolding the text of the name of the subgroup that contains the type specimen for the group.